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THE FACTORS DETERMINING THE VERTICAL MOVEMENTS OF *DAPHNIA*

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INTRODUCTION

Vertical movements of the plankton crustacea have been noted by many observers. The published results show that there is great variation in the movements made by different species, and that the same species in different lakes shows great differences in its vertical migrations. These facts indicate that there is a considerable number of factors which operate together to determine the movements. This paper is presented with the hope that it will help to make clear the relative importance of the factors determining the movements of a common fresh water entomostracean.

This study has been carried on under the direction of Dr. S. J. Holmes to whom the author is indebted for constant advice and criticism. To Professor E. P. Lewis of the Department of Physics thanks are due for information concerning the absorption of ultra-violet rays in passing through the atmosphere and through water. Dr. A. C. Chandler assisted in taking observations in some of the longer experiments.

In the following experiments only one species of crustacean was used, *Daphnia pulex* De Geer, which was found abundantly at times in the lakes and ponds about Berkeley. The specimens used were obtained from several artificial ponds on the University Campus. Many were kept for some time in glass aquaria in the laboratory before being used for experimentation in order to accustom them to laboratory conditions; others were used immediately after being collected from the pond in order to ascertain how far the behavior had been modified by the artificial conditions. It has been observed that daphnids in different stages of their life history show differences in their vertical movements. To avoid this complication only adult individuals were used.

In all these experiments the animals were kept in water taken from the same aquarium as the animals unless a statement is made to the contrary. In the experiments on geotaxis the jars were filled completely and the top sealed by a ground glass stopper to exclude the possibility of a difference of oxygen content between the top and the bottom. To avoid the possibility of chance in the animals remaining constantly at one end or the other of the dish, the ends were occasionally reversed or the contents of the dish stirred up.

The experiments were performed between August, 1913 and April, 1914 in the Zoological Laboratories of the University of California at Berkeley.

PART I. EXPERIMENTAL

PHOTOTAXIS IN RELATION TO LIGHT INTENSITY

The individuals of *Daphnia pulex* are normally positively phototactic and under conditions similar to those they would meet in nature it is difficult to obtain from them a negative response. In weak light or moderately strong light most of them are strongly positive. To the light from a 100 watt Mazda lamp at a distance of 30 centimeters they remained strongly positive throughout an exposure of nearly six hours. (Exp. 1.)

Exp. 1

Phototaxis in weak light

January 29, 8.30 A.M., 18 *Daphnia pulex* from diffuse daylight placed in a glass dish 28 cm. long marked off into five transverse divisions. Exposed in darkroom to horizontal light from 100 watt Mazda lamp at 30 cm. Temperature 17.5° C.

Divisions	Positive end I	II	III	IV	Negative end V
9.00 A.M.	*14	1	1	2	0
9.15	15	1	0	1	1
9.45	15	1	0	2	0
10.50	15	1	0	2	0
11.50	15	2	0	0	1
1.00 P.M.	14	0	1	0	3
2.00	13	3	0	1	1
2.20	13	2	1	2	0
Averages	14.2	1.4	0.4	1.2	0.8

Another experiment (Exp. 2) shows that to the weak light from a 50 watt Edison lamp at 50 centimeters the animals remain positive during a continuous exposure of 60 hours. Probably they would remain positive indefinitely to these intensities. It appears that they are more strongly positive in the stronger light.

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* The figures refer to the number of individuals in each division.

Exp. 2

Phototaxis in weak light

March 23, 4 P.M., 25 *Daphnia pulex* placed in a 28 cm. long glass dish marked off into five divisions. Exposed in darkroom to horizontal light from a 50 watt Edison lamp at 50 cm. distance. Temperature 17.5° C.

	Positive end				Negative end
Divisions	I	II	III	IV	V
Mar. 24, 4 P.M.	20	0	1	1	3
8	17	2	2	2	2
12	14	1	5	2	3
Mar. 25, 4 A.M.	10	2	3	5	5
8	13	1	5	4	2
12 M.	14	1	3	2	5
4 P.M.	10	3	5	4	3
8	10	2	6	3	4
Mar. 26, 8 A.M.	13	5	1	1	5
Averages	13.4	1.9	3.4	2.7	3.5

These daphnids, at temperatures of 20° to 23° C., are generally nearly neutral to diffuse daylight (Exp. 3), to the light from a 15 ampere electric arc (Exp. 4), or to sunlight lacking the ultra-violet rays (Exp. 5). Experiment 3 shows a rather large variation in the distribution of the animals during the experiment which is probably due to the changes in light intensity corresponding to changes in the position of the sun.

Exp. 3

Phototaxis in diffuse daylight

March 19, 8 A.M., 22 *Daphnia pulex* from laboratory aquarium placed in a 28 cm. long glass dish marked off into three divisions. Exposed to diffuse light from a south window covered by a white screen. Light rays from the room were excluded by a black lined box. Temperature 23° C.

	Positive end		Negative end
Divisions	I	II	III
8.20 A.M.	6	5	11
8.45	6	6	10
9.30	9	3	10
10.00	8	3	11
11.00	8	7	7
12.00 M.	9	8	5
1.00 P.M.	9	6	7
2.00	9	7	6
3.00	9	8	5
4.00	11	7	4
5.00	10	9	3
6.00	13	6	3
Averages	8.9	6.3	6.8

Exp. 4

Phototaxis in arc light

January 29, 18 *Daphnia pulex* which had been exposed to the light of a 100 watt Mazda lamp for four hours were placed in a glass dish 28 c.m long marked off into five divisions. Exposed them to the horizontal light from a 15 ampere electric arc at a distance of 40 cm. The light was passed through 8 cm. of water to cut out the heat.

Divisions	Positive end I	II	III	IV	Negative end V
2.30 P.M.	7	1	1	1	8
2.40	7	2	2	2	5
2.50	6	0	1	3	8
3.00	8	1	3	0	6
3.10	7	1	3	2	5
3.20	5	2	3	2	6
3.30	4	0	6	2	6
4.00	9	3	2	1	3
4.30	2	1	3	4	8
5.25	8	1	2	2	5
Averages	6.3	1.2	2.6	1.9	6.0

Exp. 5

Phototaxis in sunlight

April 13, 2 P.M., 13 *Daphnia pulex* from laboratory aquarium placed in 18 cm-long glass dish marked off into five divisions. Exposed to sunlight with ultra-violet rays cut off by one sheet of window glass. Temperature kept at 21° to 22° C.

Divisions	Positive end I	II	III	IV	Negative end V
2.05 P.M.	4	1	2	4	2
2.15	2	1	4	2	4
2.20	1	2	2	2	6
2.25	3	3	2	1	4
2.30	1	2	3	3	3
2.50	2	4	2	1	4
3.30	5	1	2	2	4
3.40	4	3	0	1	5
3.50	7	2	1	0	3
4.00	8	1	2	1	1
Averages	3.7	2.0	2.0	1.7	3.6

In these experiments it is shown that at temperatures of from 17° to 22° C. these daphnids are normally positive to weak electric light or to moderately strong light. They are more strongly positive to moderately strong light than to very weak light. The positive phototaxis to weak light persists for seemingly indefinite periods. To light intensities stronger than weak diffuse daylight these animals are indifferent and do not become negatively phototactic to any intensity of ordinary light at these temperatures.

It has been shown by Moore (1912) that *Daphnia pulex* may be made negatively phototactic by the ultra-violet rays from a mercury vapor arc lamp. The ultra-violet rays in sunlight are nearly all absorbed in passing through the atmosphere. However, experiment 6 indicates that the quantity of these rays reaching the surface of the earth at sea level (altitude of Berkeley about 100 feet) is sufficient to have a slight effect in causing negative phototaxis. In passing down through the water of a lake the ultra-violet rays will be very rapidly absorbed. In lakes at high altitudes, which receive more of these rays than lakes at sea level, and in lakes whose water is very clear the effects the negative phototaxis caused by these rays in the bright part of the day might operate to keep the daphnids down a short distance from the surface.

Exp. 6

Effect of ultra-violet rays on phototaxis

April 13, 2 P.M., 13 *Daphnia pulex* from laboratory aquarium placed in an 18 cm. long glass dish marked off into five divisions. Temperature 21° to 22° C. Exposed to sunlight with the ultra-violet rays cut off by one thickness of window glass.

Divisions	Positive end I	II	III	IV	Negative end V
2.05 P.M.	4	1	2	4	2
2.15	2	1	4	2	4
2.25	3	3	2	1	4
2.50	2	4	2	1	4
		Removed window glass			
2.51	2	1	0	0	10
2.52	0	0	0	6	7
2.53	2	0	2	3	6
2.55	2	0	2	2	7
3.10	2	0	0	4	7
3.20	3	0	2	4	4
		Replaced window glass			
3.25	4	2	2	2	3
3.30	5	1	1	2	4
Averages without ultra-violet rays:	3.3	2.0	2.2	2.0	3.5
Averages with ultra-violet rays:	1.8	0.2	1.0	3.2	6.8

Frisch and Kupelweiser (1913) state that after a short exposure *Daphnia magna* and less evidently *Daphnia pulex* become indifferent to the light and show no decided phototaxis so long as the intensity remains the same. When the light intensity is decreased the animals become temporarily positive while on increase of intensity they become temporarily negative. After a few minutes exposure to a new intensity the daphnids again become indifferent to the light and uniformly distributed throughout the dish. It has been shown above that in weak light or in light of moderate intensity *Daphnia pulex* remains constantly positive. Within the range of these intensities I have been unable to reverse even temporarily the phototaxis by sudden change of intensity. However, within the limits where the light intensity is strong enough so that the daphnids are normally indifferent, sudden changes of intensity produce the effects noted by the above mentioned authors. The tendency to these effects is probably present on any sudden change of intensity, but in weak light this tendency is overpowered by the normal phototaxis. It does not seem likely that these temporary changes of phototaxis can be of much importance in causing the vertical migrations of *Daphnia*.

PHOTOTAXIS IN RELATION TO TEMPERATURE

Loeb (1906) found that daphnids which were indifferent to light at 19° C. became positive when the temperature was reduced to 11° C. When the temperature was raised to 25° C. they became again indifferent or weakly negative. My experiments show the same results. Daphnids indifferent to sunlight at 20° C. show positive phototaxis to the same light at low temperatures. This first becomes pronounced at about 12° C. Animals positive to diffuse light showed a slight reduction of the positive phototaxis on heating to 32° C.

In diffuse light to which *Daphnia pulex* was positive at 22° C. Yerkes (1900) found no change of phototaxis on raising the temperature, although this was carried to the point where all the daphnids died. In weak or moderately weak electric light I have been unable to detect a variation in phototaxis on any amount of heating. We may then conclude that decrease of temperature causes a tendency to increase of positive phototaxis while increase of temperature causes a tendency to decrease of positive phototaxis, but that in weak light these tendencies are overpowered by the normal positive phototaxis.

The temperature at which these animals become indifferent to light varies with the light intensity. Below 15° C. they seem to be positive in any intensity. To weak light they seem positive at all temperatures. Above 25° C. in very strong light there may be a slight negative phototaxis, but if the ultraviolet rays are screened off this seems never to be at all strong.

PHOTOTAXIS IN RELATION TO THE CHEMICAL CONTENT OF THE WATER

Oxygen: No observable change in phototaxis was produced by changing daphnids from tap water containing much oxygen to the same kind of water from which the oxygen had been driven off by boiling for a half hour, or by the reverse change.

Carbon dioxide: Loeb (1906) has found that carbon dioxide will make neutral daphnids positive to light. Moore (1912) has further shown that this substance will make negative daphnids positive. This chemical then has a tendency to render *Daphnid pulex* positively phototactic.

Food: No observations are at hand bearing on the effect of food substances on phototaxis.

Waste products: A very large number of daphnids were placed in a small vessel and exposed to weak light. They remained positive to this light until the excess of organic waste products in the medium grew so great that all died.

The tendency of carbon dioxide to produce positive phototaxis seems to be the only factor in the relationship between the chemical content of the water and phototaxis that is likely to be of importance in the normal movements of *Daphnia*.

PHOTOTAXIS IN RELATION TO MECHANICAL STIMULATION

Yerkes (1900) states that some individuals of *Daphnia pulex* may be made temporarily weakly negative to light by mechanical stimulation, such as picking them up in a pipette, but with many individuals he failed to obtain this result. I have been unable to produce negative phototaxis by any amount of gentle or rough handling, either by picking the animals up in a pipette or by shaking the dish.

PHOTOTAXIS IN RELATION TO TIME OF DAY

Daphnids exposed in the darkroom to weak horizontal light from a 50 watt Edison lamp at 50 cm. distance, with observations taken each hour for 30 hours, gave no evidence of a change in phototaxis corresponding in any way to a daily period. Neither could such a change be detected in daphnids exposed for 24 hours to the same weak light before beginning the series of observations. In no experiment is there found the least evidence for believing in the existence of any sort of a rhythm in phototaxis independent of the direct effect of recurrent external changes.

GEOTAXIS IN RELATION TO LIGHT INTENSITY

When daphnids which have been kept some time in darkness are suddenly exposed to light of any intensity coming from a horizontal direction there is a tendency for them to go to the bottom of the dish (Exp. 7). Conversely, when daphnids which have been exposed to light of any intensity are placed in complete darkness they show a tendency to rise to the top of the dish. A tendency to positive geotaxis is also found on changing from weak light to stronger light (Exp. 8), or from moderately strong light to the light from an electric arc (Exp. 9). There is also a tendency of this kind on changing from shade to sunlight (Exp. 10). Negative geotaxis is produced by the reverse change in each of these cases.

Exp. 7

Effect of change of light intensity on geotaxis

March 18, 11 A.M., 14 *Daphnia pulex* from 17 hours in darkness placed in a 14 cm. high glass jar marked off into three divisions. Cooled to 13° C.

	Top		Bottom
Divisions	I	II	III
11.15 A.M.	8	1	5
11.30	9	0	5
11.45	8	1	5
11.50	5	2	7
Turned on light of a 40 watt Edison lamp at a horizontal distance of one meter.			
11.51	2	2	10
11.52	0	2	12
11.53	0	1	13
11.54	0	0	14
11.55	0	0	14
Light turned off.			
12.00	7	0	7
Averages in darkness:	7.4	0.8	5.8
Averages in light:	0.4	1.0	12.6

Exp. 8

Effect of change of light intensity on geotaxis

January 20, 2.30 P.M., 11 *Daphnia pulex* from diffuse light of laboratory placed in a 29 cm. high jar marked off into five divisions. Top sealed. For weak light used horizontal light from a 40 watt Edison lamp at 2 meters, and for strong light used a 100 watt Mazda lamp at a horizontal distance of 20 cm.

Divisions	Top I	II	III	IV	Bottom V
		Weak light			
2.45 P.M.	1	3	4	1	2
2.50	2	2	2	2	3
2.55	3	2	2	2	2
		Strong light			
3.00	0	0	0	0	11
3.05	0	2	0	1	8
3.10	1	1	1	2	6
3.15	1	0	2	0	8
3.20	1	2	1	3	4
3.25	1	2	1	1	6
3.45	0	1	1	1	8
		Weak light			
3.55	7	1	2	0	1
4.00	9	1	2	0	1
4.10	6	2	1	1	1
4.20	7	2	0	0	2
4.45	5	3	0	0	3
		Strong light			
4.50	0	0	0	0	11
4.55	1	0	0	1	9
5.00	2	2	0	0	7
		Weak light			
5.05	8	1	0	1	1
5.10	10	0	0	0	1
		Strong light			
5.11	0	0	0	0	11
5.15	2	1	1	1	6
		Weak light			
5.20	10	0	0	0	1
		Strong light			
5.21	2	1	1	0	7
5.25	5	0	0	1	5
		Weak light			
5.30	10	0	0	0	1
5.40	8	0	0	1	2
5.50	8	0	0	0	3
		Strong light			
5.55	1	0	1	1	8
6.00	2	0	1	0	8
Average in weak light:	6.7	1.1	0.9	0.5	1.8
Average in strong light:	1.2	0.8	0.6	0.8	7.7

Exp. 9

Effect of change of light intensity on geotaxis

January 29, 2 P.M., 50 *Daphnia pulex* collected from pond and placed in a 29 cm. high jar marked off into five divisions. Top sealed. For strong light used a 15 ampere electric arc at 40 cm. and for weak light used a 100 watt Mazda lamp at 40 cm. The light was horizontal in each case and was passed through 8 cm. of water to cut out the heat.

	Top				Bottom
Divisions	I	II	III	IV	V
3.11 P.M.	Strong light turned on.				
3.14	1	2	6	10	31
3.24	2	4	5	12	27
3.29	4	3	10	10	23
3.44	1	2	5	10	32
3.54	2	3	4	10	31
4.04	0	3	5	10	32
4.24	2	2	3	10	33
4.44	1	3	5	8	33
4.49	1	4	7	10	28
		Weak light			
4.54	24	10	5	4	7
4.59	21	10	4	7	8
		Strong light			
5.04	1	3	2	8	36
5.14	2	1	5	8	34
5.24	1	1	4	10	34
Averages in strong light:					
	1.5	2.6	5.1	9.7	31.1
Averages in weak light:					
	22.5	10.0	4.5	5.5	7.5

Exp. 10

Effect of change of light intensity on geotaxis

March 26, 17 *Daphnia pulex* in diffuse light of laboratory placed in 29 cm. high jar marked off into five divisions. Cooled to 13° C.

	Top				Bottom
Divisions	I	II	III	IV	V
9.10 A.M.	4	2	1	1	9
9.11	Exposed to sunlight. Jar inclined at right angles to the rays.				
9.12	0	0	0	1	16
9.13	0	0	0	0	17
		Placed in shade			
9.14	0	0	0	1	16
9.15	0	1	4	1	11
9.16	3	1	1	1	11
9.20	4	0	1	4	8
Averages in shade:					
	2.2	0.8	1.4	1.6	11.0
Averages in sunlight:					
	0.0	0.0	0.0	0.5	16.5

The tendency to go to the bottom on increase of light intensity cannot be due to a decrease of locomotor activity as it has been shown by Yerkes (1900) that the locomotor activity increases with increase of light intensity. Neither can it be due to a change of phototaxis because it takes place when the light comes from a horizontal direction. Further, it can be observed that following a great increase of light intensity many of the animals swim directly downwards with the head pointed toward the bottom of the dish. It seems that we have to do here with a change of some sort in the orientation of the animals to the force of gravity. The tendency to move upward following a decrease of intensity is also well marked and must also be due to a change in the reaction of the animals to gravity.

Exp. 11

Independence of geotaxis caused by change of light intensity from phototaxis

February 19, 8.15 A.M., 18 *Daphnia pulex* from 14 hours in darkness placed in a 29 cm. high jar marked off into five divisions. Exposed to the horizontal light from a 15 ampere electric arc at 50 cm. distance.

Divisions	Top I	II	III	IV	Bottom V
8.46 A.M.	0	0	0	0	18
8.47	0	0	2	8	8
8.50	0	0	1	3	14
Arc moved to a position above at an angle of 45 degrees					
8.56	0	0	0	1	17
9.00	0	2	2	5	9
9.02	0	0	1	4	13
9.05	0	0	1	5	12
Arc moved back to horizontal position					
9.15	0	0	0	1	17
9.20	0	0	0	2	16
Arc below at angle of 45 degrees					
9.25	0	4	3	2	9
9.30	0	3	3	4	8
9.35	1	1	4	6	6
9.40	0	2	5	4	7
Arc back to horizontal position					
9.45	0	0	3	3	12
10.00	0	2	1	3	12
10.45	0	2	2	2	12
Arc off. On light of 40 watt Edison at 50 cm. horizontal					
10.50	1	4	5	1	7
11.00	5	4	1	2	6
11.15	5	7	3	1	2
11.25	9	2	1	1	5

Proof that the reversal of geotaxis by changes in light intensity is independent of phototaxis is given in Experiment 11. Here the daphnids remained at the bottom of the dish when exposed to the light from an arc light, no matter whether the light was falling from the side or at an angle of 45 degrees from above or below. When exposed to weak light following the exposure to the arclight the daphnids showed a strong upward tendency indicating that the effect on geotaxis in this case was undoubtedly due to the light intensity.

Experiment 12 is presented to show that the vertical distribution remains altered for a long time after reduction of light intensity.

Exp. 12

Persistence of negative geotaxis in darkness

March 28, 8.30 A.M., 10 *Daphnia pulex* from laboratory aquarium at a temperature of 18.5° C. placed in a 29 cm. high jar marked off into five divisions. Exposed to diffuse light of laboratory. Cooled to 13° C.

	Top				Bottom
Divisions	I	II	III	IV	V
9.30 A.M.	1	1	2	2	4
10.00	1	5	0	0	4
10.30	0	1	2	3	4
11.00	3	2	2	0	3
		Placed in darkness			
11.30	6	1	0	0	3
12.00 M.	5	2	1	0	2
1.00 P.M.	3	2	0	2	3
2.00	4	1	1	1	3
3.00	5	1	1	0	3
4.00	6	1	0	1	2
Averages in light at 13° C.:	1.2	2.3	1.5	1.2	3.8
Averages in darkness at 13° C.:	4.8	1.3	0.5	0.7	2.7

We have shown that in *Daphnia pulex* increase of light intensity causes a tendency toward positive geotaxis, while decrease of intensity causes a tendency toward negative geotaxis. This tendency seems to be stronger the greater the change in intensity. It seems also that these tendencies are persistent for a considerable length of time.

GEOTAXIS IN RELATION TO TEMPERATURE

On heating *Daphnia pulex* in the dark to a temperature of about 25° C. there is a strong tendency for the animals to go to the bottom of the dish (Exp. 13). On cooling them to a temperature of about 15° C. there is a tendency for them to go to the surface (Exp. 14). The position of these animals kept in the dark was determined by turning on a weak light and taking the observation before the position of the animals could change. The tendency to go down on heating cannot be due to the effect of temperature on the locomotor activity, because it will be shown in a later section that increase of temperature causes an increase of locomotor activity which would tend to cause the animals to move upwards. Neither can this tendency be due to any effect of light because the tendency is present in the complete absence of light. Seemingly it is due to a change in the orientation of the animals with respect to gravity. We may then suppose that the tendency to move upward on cooling is also due to a change in the relation of the animals to the force of gravity. In horizontal light the same effect of temperature on geotaxis is found (Exp. 15).

Exp. 13

Positive geotaxis caused by heating

March 19, 8 A.M., 10 *Daphnia pulex* from 14 hours in darkness placed in a 29 cm. high jar marked off into three divisions. Kept in complete darkness except when making observations. Temperature 21° C.

	Top		Bottom
Divisions	I	II	III
8.15 A.M.	4	4	2
8.45	1	2	7
	Heated to 26° C.		
9.00	2	0	8
9.30	0	0	10
10.00	0	2	8
11.00	0	3	7
12.00 M.	0	1	9
1.00 P.M.	1	2	7
2.00	1	1	8
3.00	0	1	9
4.00	0	2	8
5.00	0	0	10
6.00	1	1	8
Averages at 21° C.:	2.5	3.0	4.5
Averages at 26° C.:	0.5	1.2	8.3

Exp. 14

Effect of temperature on geotaxis

March 19, 8 A.M., 10 *Daphnia pulex* kept 14 hours in darkness placed in a 29 cm. high jar marked off into three divisions. Still in complete darkness. Temperature 21° C.

	Top		Bottom
Divisions	I	II	III
8.15 A.M.	2	1	7
8.45	1	1	8
Cooled to 13° C.			
9.00	6	0	4
9.30	3	0	7
10.00	3	1	6
11.00	5	1	4
12.00 M.	6	0	4
1.00 P.M.	4	3	3
2.00	6	0	4
3.00	4	2	4
4.00	3	0	7
5.00	3	0	7
6.00	3	0	7
Averages at 21° C.:	1.5	1.0	7.5
Averages at 13° C.:	4.2	0.6	5.2

Exp. 15

Effect on geotaxis of change in temperature

February 26, 15 *Daphnia pulex* 15 hours in darkroom exposed to horizontal light from an 80 watt Edison lamp at 2 meters placed in a 29 cm. high jar marked off into five divisions. Experiment in same light.

	Top				Bottom	
Divisions	I	II	III	IV	V	
8.55 A.M.	4	2	0	4	5	19° C.
9.00	4	3	0	2	6	
Heated to 25° C.						
9.15	0	1	2	1	11	25° C.
9.30	2	2	1	1	9	
9.45	1	0	1	4	9	26° C.
10.00	2	1	1	0	11	
10.15	2	3	0	2	8	
10.30	2	0	2	1	10	
10.45	2	0	1	2	10	25° C.
Cooled to 17° C.						
11.00	0	3	2	5	5	17° C.
11.15	6	0	0	5	4	14° C.
11.15	6	0	0	5	4	14° C.
11.30	5	3	1	2	4	
11.45	4	4	4	0	3	14.5° C.
12.00 M.	6	2	1	2	4	
Averages at low temperatures:	4.1	2.4	1.2	2.9	4.4	
Averages at high temperatures:	1.6	1.0	1.1	1.6	9.8	

The normal vertical position of daphnids exposed to horizontal light or to darkness will be determined, first by the geotaxis, which will vary with the light intensity and the temperature; and second, by the rate of locomotor activity, which will also vary with the light intensity and with the temperature. The relations of these factors is very complex, especially in view of the fact that the previous exposure to light and heat must be taken into account. Experiments 13 and 14 show that the tendency to go down on heating and up on cooling is persistent for a number of hours.

In general, high temperatures produce in *Daphnia pulex* a tendency to positive geotaxis, while low temperatures produce a tendency to negative geotaxis. These tendencies persist for at least a considerable length of time.

GEOTAXIS IN RELATION TO THE CHEMICAL CONTENT OF THE WATER

Oxygen: No definite change in vertical distribution could be observed on changing daphnids from water saturated with oxygen to water from which the oxygen had been driven off by boiling or by the reverse change.

Carbon dioxide: Carbon dioxide gas was bubbled for half an hour through a jar of tap water and this was then supposed to contain an extra amount of the chemical in solution. How ever, no change in the vertical distribution could be observed on changing daphnids into this water or back into normal tap water.

Food: No experiments were conducted on the effect of food as a factor affecting geotaxis, but it is probably not of importance in this respect.

Waste: One experiment was performed on the effect of waste materials on geotaxis. A very large number of daphnids were placed together in a tall sealed glass jar in the darkroom with weak horizontal light. The crowding was so great that all the adults had died before the end of 24 hours. During this time no change in geotaxis could be observed so it seems that organic waste products have little effect on geotaxis.

In so far as these observations and inferences are conclusive we find that changes in the chemical content of the medium have little effect on the geotaxis of the adults of *Daphnia pulex.*

GEOTAXIS IN RELATION TO MECHANICAL STIMULATION

It could not be determined that mechanical stimulation has any effect on the geotaxis of these daphnids. If such an effect is present it is either very weakly marked or is very temporary and can have little value in determining the vertical movements of the animals.

GEOTAXIS AT DIFFERENT TIMES OF THE DAY

A number of experiments were performed to determine if the geotaxis varies at different times during the day. The method used was to place a number of daphnids in a tall jar marked off into five divisions. The jar was completely filled with water and the top sealed by a glass stopper. In the darkroom the jar of animals was exposed to weak horizontal light. A count was made each hour of the number of individuals in each division of the jar, during a period of 30 hours. No periodicity in vertical distribution could be found, either in daphnids taken from daylight at the beginning of the experiment or in daphnids previously exposed to weak light for a day or more. We may then conclude that there is no diurnal rhythm of geotaxis in this species, except that dependent upon rhythmical change in the external physical factors.

LOCOMOTOR ACTIVITY IN RELATION TO LIGHT INTENSITY

Daphnids under natural conditions assume a position in the water with the head pointing upward. When no locomotor movements are being made the drag of the antennae on the water, as the weight of the body pulls the animal down, causes the daphnids to assume this posision. When strokes are made with the antennae the tendency then is to raise the animal vertically through the water.

The rate of sinking of adult daphnids 3 to 4 millimeters long with expanded antennae is stated by Birge (1897) to be at the rate of 20 to 30 centimeters per minute. Young daphnids 1 millimeter or less in length sink much more slowly at the rate of 5 to 10 centimeters per minute. This slower rate of sinking makes it much easier for the young daphnids to remain near the surface than it is for the adults.

It will be seen that it requires a certain rate of activity to maintain an individual at any certain height in the water. If the locomotor activity increases there will be a tendency for the animal to move to higher levels while a decrease of activity will allow it to sink.

Yerkes (1900) has shown that an increase of light intensity increases the speed of locomotion in *Daphnia pulex*. It can easily be observed that on a great increase of light intensity there is a decided increase of activity.

The increase of locomotor activity caused by increase of light intensity will have a tendency to cause the daphnids to move upwards, while a decrease of intensity slows down their activity and allows them to sink to lower levels.

LOCOMOTOR ACTIVITY IN RELATION TO TEMPERATURE

In studying the effect of temperature on locomotor activity a number of experiments were performed to determine the speed of motion toward a weak light at various temperatures. This method is not very satisfactory because the change in temperature causes changes in the phototaxis as well as in the locomotor activity and it is difficult to separate the effects of the two factors. Further, different individuals give very different and often contradictory results. The number of animals used in the averages is too small to give very great accuracy in conclusions. However, it is thought that some of the relations between temperature and rate of activity are indicated.

The method used was to mark off transverse lines 10 centimeters apart on the bottom of a glass dish. In the darkroom a 50 watt Edison lamp was placed 25 centimeters horizontally from each end of the dish. A daphnid was then introduced into the dish and allowed to swim toward one light. As soon as the animal passed the line marked off on that end of the dish this light was turned off and at the same time the light at the other end of the dish turned on. An observation consisted of 8 trips, 4 each way, of the animal across the dish. The time was recorded in minutes and seconds. In comparing the effects of change of temperature two dishes were used with the water kept at the different temperatures. Then the animals were gently shifted from one to the other by a large pipette.

In Experiment 16 each individual shows a decided increase of speed of travel toward a weak light on first raising the temperature 5 degrees. The averages for five individuals are 4′ 02″

at normal temperature and 2′ 46″ after heating. Also, the averages of all the observations show a higher rate of speed at the higher temperature. This effect is produced in spite of the fact that the phototaxis is lessened by the increase of temperature. In this case then we have a definite increase of locomotor activity by increase of temperature.

Exp. 16

Effect of heating on rate of locomotor activity

Time in minutes and seconds required to travel 80 cm. toward a weak light.

Temperature, C....	20.5°	25.5°	20.5°	25.5°	20.5°
Individual A	3′ 23″	2′ 50″	1′ 55″	2′ 23″	1′ 45″
B	2′ 20″	2′ 05″	1′ 05″	1′ 30″	1′ 45″
C	5′ 00″	3′ 00″	3′ 00″	2′ 25″	3′ 15″
D	4′ 55″	3′ 20″	4′ 40″	3′ 20″	4′ 55″
E	4′ 35″	2′ 35″	3′ 05″	1′ 55″	2′ 45″
Averages..........	4′ 02″	2′ 46″	2′54″	2′ 18″	2′ 39″

Average speed before change of temperature, 4′ 02″.
Average speed on first heating, 2′ 46″.
Average speed at 25.5° C., 2′ 32″.
Average speed at 20.5° C. after heating, 2′ 46″.

On cooling daphnids from a normal temperature of 20° C. down to 15° C. there is also an increase of speed of motion toward a weak light and the averages show very definitely a faster rate of speed at the low temperature than at the normal. However, the decrease of temperature increases the positive phototaxis and the increase in speed of travel may be due to this cause rather than to the lower temperature directly increasing the locomotor activity.

Experiment 17 shows the effect of continued exposure to a temperature of 25.5° C. This indicates that while the activity is increased when the temperature is first raised, after a short time the speed of travel decreases and soon the animal travels more slowly than at the normal temperature. It can be directly observed that a continued high temperature causes many of the daphnids to become very weakly positive and to show many erratic movements, even going at times directly away from the light. Many also grow very feeble and show a tendency to settle to the bottom of the dish. This is a real decrease of locomotor activity. However, other individuals show a continued high rate of locomotion after a lengthy exposure to the higher temperature.

Exp. 17

Activity on continued exposure to high temperature

Time in minutes and seconds required to travel 80 cm. toward a weak light.

Temperature, C....	20.5°	25.5°					
Exposure, minutes..		0	15	30	45	60	90
Individual A	3′ 20″	3′ 08″	3′ 35″	2′ 10″	6′ 35″	5′ 20″	8′ 05″
B	3′ 05″	2′ 00″	2′ 17″	2′ 30″	3′ 15″	3′ 00″	2′ 10″
C	2′ 30″	2′ 10″	1′ 40″	1′ 30″	1′ 30″	1′ 35″	2′ 00″
D	3′ 30″	3′ 55″	4′ 40″	4′ 50″	6′ 30″	3′ 25″	5′ 00″
E	2′ 05″	2′ 20″	2′ 40″	3′ 15″	2′ 30″	3′ 00″	3′ 55″
Averages..........	2′ 54″	2′ 43″	2′ 58″	2′ 51″	4′ 04″	3′ 16″	4′ 14″

The effect of continued exposure to cold seems to be very irregular. Some individuals show a decrease of speed of travel on continued exposure to a temperature of 15° C., while others show an increase of activity under the same conditions. The results are too uncertain to base any definite conclusions upon.

Temperature, then, has a very irregular effect on locomotor activity. The most definite fact is that a sudden increase of 5 degrees above the normal causes an increase of activity, which persists for a short time.

LOCOMOTOR ACTIVITY IN RELATION TO THE CHEMICAL CONTENT OF THE WATER

The chemical content of the water is probably of importance in modifying the rate of locomotion of these animals, but no experiments bearing on this subject have been performed. As the chemical content of the water is subject to very little daily variation this factor cannot be a primary factor affecting diurnal migration although it might have some effect on the seasonal migrations.

LOCOMOTOR ACTIVITY IN RELATION TO MECHANICAL STIMULATION

Observations show that by strong mechanical stimulation, such as caused by shaking the dish, the locomotor activity is temporarily stopped. This allows the animals to sink downward. On the cessation of the stimulation the activity is, for a short time, greater than before.

LOCOMOTOR ACTIVITY AT DIFFERENT TIMES OF DAY

Experiments performed to determine whether a periodicity in vertical distribution occurred gave only negative results (see geotaxis in relation to time of day). The possibility may be considered that both geotaxis and activity have diurnal rhythms and that the activity decreases in the same degree that the negative geotaxis increases and the reverse. Such a condition is not believable. We may then feel confident that there is no diurnal rhythm in either, except such as is due to daily changes in the external physical factors.

THERMOTAXIS

Yerkes (1903) has shown that the radiant heat from a 16 candle-power incandescent lamp does not have an appreciable effect on the movements of *Daphnia pulex.* In darkness there is an irregular wandering away from a region heated to 29° C. This will evidently be of some importance in determining the vertical positions of the animals in lakes where the surface layers grow very warm in summer.

CHEMOTAXIS

No observations have been made as to the possibility of chemotaxis being a factor in the vertical movements of *Daphnia.* It can hardly be a very important factor, although it might have a modifying influence on behavior.

PRESSURE

The pressure acting at any given depth in a body of water will be very nearly constant at all times so that pressure changes cannot be a primary factor determining the movements of the plankton crustacea. As the animals move upward or downward in response to various other tendencies the changes in pressure experienced might be supposed to modify to some extent the action of these tendencies. However, the only experiment performed to test this supposition gave negative results. In this experiment an increase in water pressure roughly guessed at 15 pounds did not seem to cause any change in the vertical distribution of the animals. The extensive daily migrations performed by some species of *Daphnia*, 32 meters in *Daphnia hyalina* (Burckhardt, 1900), also argues against pressure being of importance in modifying the factors causing the vertical movements in this genus.

PART II. DISCUSSION

OBSERVED VERTICAL MOVEMENTS IN *DAPHNIA*

Below are given brief statements of some of the recorded observations of vertical movements in *Daphnia*, with especial reference to *Daphnia pulex*.

Juday (1904) found that in Oconomowoc Lake, Wis., in August the adults of *Daphnia pulex pulicaria* were at a depth of 10 meters in the daytime and reached the surface an hour after sunset. In doing so they moved up into water that was at least 15° C. warmer than that occupied by them during the day. At this time the young were found at a depth of 6 meters in the daytime, and reached the surface a half hour after sunset. Neither adults nor young were taken in a surface catch made an hour and a half before sunrise. In October, adults were found 13 meters below the surface in the daytime and were taken in a surface catch made two hours after sunset. In June, both adults and young were found at a depth of 1 meter in the daytime. The young reached the surface in the first half hour after sunset and the adults arrived there a half hour later. Both left the surface during the second half hour before sunrise.

In Okauchee Lake, Wis., in August, "young were found at a depth of 8 meters and adults at 9 meters in the daytime. Two and a quarter hours after sunset young were found at a depth of only 2 meters and adults 4 meters. In October, young were at a depth of 6 and adults 12 meters in the daytime. Three and a quarter hours after sunset the former were at the surface and the latter at 2 meters. In June, the day catches showed young at a depth of 1 meter and adults at 3 meters. The former appeared at the surface about half an hour before sunset and the latter about two hours after sunset. Both disappeared from the surface during the fifth half hour before sunrise."

Little indication of a diurnal movement by *Daphnia pulex pulicaria* was found by Juday (1902) in Winona Lake, Indiana.

In Lake Mendota, Wis., Birge (1895) found no diurnal movement in this species during the month of July. During that month the species was confined in the vertical space between depths of 6 and 15 meters, and very few were below 12 meters. In this lake the young of the species show a tendency to collect in the upper parts of the lake while the adults are found at lower levels (Birge, 1897).

Juday (1904) was also unable to find a diurnal movement of this species in Lake Mendota.

The seasonal movement of *Daphnia pulex pulicaria* is well marked in Lake Mendota. Table I, based on figures given by Birge (1897), shows that in winter the species is most abundant at the surface, but that as the water of the lake heats up the animals move downward until in August they are most abundant at depths of between 9 and 12 meters. In the fall they move upward until they again appear at the surface.

TABLE 1

Daphnia pulicaria

Percentage vertical distribution in Lake Mendota, Wis.
(From Birge, 1897, *Trans. Wis. Acad. Sci.*, Vol. 11.)

		Per cent. in each 3 meter level					
Depth, meters . . .		0–3	3–6	6–9	9–12	12–15	15–81
1895–1896							
July	16–31	0.0	0.0	53.1	12.5	32.8	1.6
August	1–15	0.0	0.0	11.0	65.0	22.0	1.0
August	16–31	0.0	1.6	2.3	80.2	14.8	1.0
September	1–15	0.0	2.2	4.5	68.8	22.6	1.8
September	16–30	0.0	1.5	2.2	3.4	58.8	33.7
October	1–15	14.1	13.8	14.1	19.2	17.1	21.7
October	16–31	22.5	21.9	22.3	12.7	9.6	11.0
November	1–15	42.7	27.3	8.7	9.2	5.5	6.6
November	16–30	25.2	29.2	19.6	15.1	5.7	5.2
December	1–15	51.6	35.5	7.9	2.8	1.9	0.2
December	16–31	37.8	31.1	11.4	11.1	7.7	0.9
January	1–15	68.3	14.5	12.7	3.5	0.5	0.5
January	16–31	77.9	8.4	8.4	2.1	2.1	1.1
February	1–14	75.8	9.1	5.0	2.8	2.4	4.8
February	15–29	43.4	20.3	8.7	11.5	8.7	7.3
March	1–15	....	....	....	....	....	....
March	16–31	34.0	18.9	27.0	9.4	7.6	3.2
April	1–15	10.4	14.6	31.2	25.0	12.5	6.3
April	16–30	84.9	10.6	0.8	1.5	1.7	0.5
May	1–15	13.1	16.2	19.5	12.0	16.7	22.4
May	16–31	28.0	16.9	18.8	14.5	10.0	11.7
June	1–15	17.5	10.0	15.0	21.3	10.1	25.8
June	16–30	1.9	6.2	11.7	16.0	45.8	18.5
July	1–15	0.0	0.9	8.6	27.0	57.0	6.5
July	16–31	0.0	0.0	62.8	33.4	2.0	1.8
August	1–15	0.0	10.0	17 0	71.0	2.0	0.0
August	16–31	0.0	0.0	0.0	80.0	20.0	0.0

On August 26, 1985, there was an alternation of cloud and sunshine over Lake Mendota and Birge (1897) observed that adult and young daphnids were approximately one meter below the surface during the sunny periods, but rose to one-half meter during the cloudy intervals. "The rise immediately followed the obscuring of the sun and the return was as prompt when the sun shone again."

The same author (1897) was unable to find that wind and waves affect the distribution of the plankton crustacea. The upper meter was fully occupied by them when the lake was almost too rough to venture out in a row boat. These results do not agree with those of Francé (1894), who found that in stormy weather the crustacea were found at a greater depth than during still weather.

In those lakes where the water in the lower levels becomes stagnant at certain periods in the year the crustacea are usually found to be entirely absent below the thermocline (Birge 1897). In these lakes the daphnids in their seasonal migrations move down, closely following the downward movement of the thermocline.

In the Vierwaldstättersee, Burckhardt (1900) observed a diurnal movement of *Daphnia hyalina* of about 32 meters during the early part of September. The mean depths of these daphnids at different times in the day on September 1st and 2nd are given below:

9 P.M. to 4 A.M. at 5 meters.
at 9 A.M. at 30 meters.
at 12 M. at 37 meters.
at 5 P.M. at 28 meters.

From the above observations, we find that there is often a diurnal migration in *Daphnia*, and that in such cases the animals are found nearest the surface at night and deeper in the lake during the day. This diurnal migration varies greatly in extent in different lakes and in different seasons. In Oconomowoc Lake, during October, there is a diurnal movement from a depth of 12 meters to the surface, while in the same lake in June the movement is only from a depth of 1 meter to the surface. In some lakes there is only a slight diurnal movement, while in others no diurnal movement has been found.

In many lakes there is an annual movement, which may be illustrated by the movement of *Daphnia pulex pulicaria* in Lake Mendota. Here the animals have a definite vertical range in the water at each season, this being near the surface in winter and deeper in the lake during the summer. Diurnal movement may occur at all seasons, but is confined within the limits of the range for the given season, so that at some seasons the diurnal movement does not reach the surface at any time during the day.

There is a marked difference between the movements of the adults and the young daphnids. The young animals are nearly always found nearer the surface than the adults, and move upward more promptly than the latter.

Storms cause the plankton crustacea to be found at lower depths according to some observers, but this does not seem to be always the case.

Cloudy weather causes the daphnids to be found nearer the surface than would be the case in clear weather.

Moonlight has been stated to result in driving the plankton crustacea to lower depths than the normal for a dark night.

These, then, are the movements of *Daphnia* whose causes are the object of study in this paper. While it will be impossible to discuss the factors governing the movements in each lake, because the physical factors have not been studied in sufficient detail, still, on the basis of the experiments described in the first part of this paper, it will be possible to suggest in many cases the probable relationship between the physical factors and the observed movements.

VERTICAL MOVEMENTS CAUSED BY CHANGES OF LIGHT INTENSITY

As sunlight passes down through the water of a lake it is gradually absorbed until at great depths there is absolute darkness. This result gives, in deep lakes, a range of light intensities from full sunlight to darkness. We have seen that *Daphnia pulex* is positively phototactic at intensities below the intensity of diffuse daylight. To intensities above this, at a temperature of 20° C., the animals are normally neutral. Only in high temperatures and strong light do they show a negative phototaxis. The positive phototaxis of the daphnids will prevent them from going much below the lower limit of neutral intensity, but, as far as the phototaxis is concerned, they might occur at any level in the neutral intensity. The range of light intensity to which the daphnids are neutral must extend over a considerable depth.

It has also been shown that the light intensity affects the geotaxis. The action of the positive geotaxis induced by strong or moderately strong light will probably be to cause the daphnids to go down until further motion downward is stopped by the beginning of positive phototaxis.

The most important change in light intensity acting on a lake is the change from sunlight to darkness occurring every day. If we suppose the daphnids to be at the surface at night, the first rays of light in the morning will cause a positive geotaxis which will overcome to some extent the positive phototaxis and the animals will begin to move downward. As the light increases in intensity they will continue to move downward, owing to the continued increasing positive geotaxis, and will keep near the lower limit of neutral phototaxis. The downward movement then is due to the action of light on the geotaxis, but the limit of downward motion is determined partly by the phototaxis. In the evening as the daylight fades the daphnids move upward, owing partly to the negative geotaxis caused by lowered light intensity, and partly due to the positive phototaxis caused by weak light. At night the daphnids remain near the surface due to the negative geotaxis existing in the absence of light. For the sake of simplicity in the above statement no account has been taken of the gradual changes in light intensity throughout the day.

It is evident that in the case of *Daphnia pulex* the change of geotaxis caused by changes in light intensity is the most important factor causing the diurnal migrations, while change of phototaxis is a factor merely limiting the extent of the movements. If there were no change in geotaxis there would be only a feeble indication of a diurnal migration in this species.

The reversal of phototaxis caused by the action of the ultraviolet rays might under some circumstances be a factor causing diurnal movement, but it seems that in this case the positive geotaxis caused by the action of the visible rays will keep these daphnids down below the action of the ultra-violet rays, so that the action of these rays will not be a factor in the vertical movements.

The light intensity effective on any given lake will vary at different seasons of the year. The lower limit of neutral light intensity for phototaxis should be at a much lower depth at midday in summer than at the same time of day in winter. For this reason the lower limit of daily movement in *Daphnia* should be deeper in summer than in winter. However, the range of motion may be less in summer than in winter owing to the effect of the higher temperatures of the surface waters in summer on the geotaxis. It seems that the change of the midday light intensities with the seasons will have a much smaller effect in determining the mean daily depth than will the changes in temperature.

Cloudy weather should have the effect of raising the mean vertical position of the daphnids. In partly clouded weather the passage of a cloud across the sun should reduce the light intensity enough to cause a tendency to negative geotaxis and positive phototaxis which would cause an upward movement of the animals. Clear sunshine following would produce a tendency to positive geotaxis and neutral phototaxis resulting in movement downward.

Very strong moonlight might cause a slight tendency to positive geotaxis and produce a small movement downwards.

Different lakes will be subjected to great differences in light intensity due to their position in latitude and altitude. The light will penetrate to very different depths in different lakes owing to the great variation in the clearness of the water. We should then not expect to find the same migration behavior in every lake.

VERTICAL MOVEMENTS CAUSED BY CHANGES IN TEMPERATURE

Few observations are at hand to show the variation during the day of the water temperatures at different levels in a lake, but this variation is much greater in shallow than in deep lakes. A table given by Hankinson (1907, p. 202) shows a variation of three degrees in the surface temperature, during May 29, in a shallow part of Walnut Lake, Michigan. The daily variations in temperature of some shallow lakes must be greater than this, but in most lakes the variation in the temperature of the surface water will be very small and there will be almost no diurnal variation in the temperature of the lower levels. Temperature changes, then, cannot have an important influence in causing the diurnal movements.

In summer the surface waters of an ordinary lake become warmed while, if the lake be deep enough, the lower levels remain cool (Table II).

TABLE II

Temperatures of Lake Cochituate, Mass.
(From Fitzgerald, 1893, *Trans. Amer. Soc. Civ. Eng.* 34(p. 96.)
(In degrees Centigrade calculated from the original Fahrenheit.)

Depth in feet	0	5	10	15	20	25	30	40	50	60
April 18	5.5°C.	5.5°C.	5.5°C.	5.5°C.	5.5°C.	5.5°C.	5.5°C.	5.6°C.	5.6°C.	5.7°C.
May 16	15.2	14.7	11.9	9.3	9.0	8.9	8.5	8.3	8.3	7.5
June 20	22.7	22.5	21.9	17.9	17.5	14.4	9.3	8.6	8.3	7.4
July 18	24.6	23.9	23.8	18.0	11.4	10.1	9.1	8.6	7.9	7.2
August 15	23.7	23.4	21.9	20.6	13.3	11.8	9.4	8.4	7.7	7.2
September 19	18.4	18.4	18.4	18.1	14.6	12.1	10.7	9.2	9.2	7.1
October 17	13.6	13.6	13.6	13.6	13.5	12.4	11.5	8.8	7.9	7.2
November 21	7.2	7.2	7.2	7.2	7.2	7.2	7.2	7.2	7.2	7.3
Averages....	16.9	16.6	16.0	14.2	11.5	10.3	9.3	8.3	7.9	7.2

It is evident that in performing any considerable migration near the surface in summer the daphnids will be subjected to a considerable variation of temperature. If we consider them moving downward in the early morning in response to increase of light intensity they will be moving into water at lower and lower temperatures. These low temperatures will have a tendency to produce negative geotaxis and positive phototaxis. These tendencies will operate to reduce the range of the downward movement. On moving upward in the evening the animals will be reaching increasing temperatures of water. These higher temperatures will have a tendency to produce positive geotaxis. If the surface temperature is in the neighborhood of 25° C. there will be a slowing up of the locomotor activity after a short exposure to that amount of heat. Irregular wandering away from the high temperature may also be operative. These factors will then work together to lessen the distance of upward travel in summer. Then, in a lake where the surface water is much warmer than the under layers we would expect that the range of diurnal migration would be much reduced.

In winter, when all the water of the lake is at nearly the same temperature we would expect rather large migrations

However, the sunlight is much reduced at that season, causing a tendency toward positive phototaxis. Also, the low temperature of the water causes a tendency toward negative geotaxis and positive phototaxis. All of these factors tend to keep the animals near the surface at all times and so cut down the range of migration at that time of year.

In different lakes the conditions of temperature will be very varied and this will have a great effect in causing the observed variations in the range and the peculiarities of the diurnal migration found in different lakes. The differences in the temperatures are particularly great between shallow and deep lakes.

As stated above, the low water temperatures of winter will have a tendency to keep the daphnids near the surface. In summer the increase in temperature of the surface layers will cause the animals to occupy lower levels. Diurnal movements may take place in summer as well as in winter, but in summer the limit of movements will be at lower levels than in winter.

Changes in temperature, then, are not the primary cause of diurnal movement, but difference in temperature of the water at different levels in a lake may operate to shorten the distance of the diurnal movement. Changes in water temperature, particularly of the surface layers, at different seasons of the year is the principal factor determining the seasonal movements. This result is chiefly due to the effect of different degrees of temperature on geotaxis, although the effect of temperature on phototaxis has a minor effect.

MOVEMENTS CAUSED BY MECHANICAL STIMULATION

The mechanical stimulation most likely to affect the plankton crustacea will be the action of the waves. It has been stated in a previous section that mechanical stimulation, while it continues, tends to inhibit the locomotor activity of the animals so that they fall passively through the water. After descending to a depth where the wave action could no longer be felt the daphnids would tend to rise again until stopped by reaching a region of perceptible wave action. The result is that the daphnids should be found at a lower level than normal on stormy days, and by this reaction escape the damaging action of strong waves.

VERTICAL MOVEMENTS CAUSED BY CHANGES IN THE CHEMICAL CONTENT OF THE MEDIUM

The chemical content of the water of an ordinary lake will be subject to changes in the proportion of dissolved food substances, in oxygen content, in the amount of dissolved carbon dioxide, and in the proportion of organic waste products.

Changes in the proportion of carbon dioxide is the only factor likely to be of importance in the vertical movements of *Daphnia*. This substance has a tendency to produce positive phototaxis. In the stagnant water found at certain seasons below the thermocline in some moderately deep lakes, the excess of carbon dioxide will perhaps increase the positive phototaxis of the daphnids enough to cause them to rise to a better ventilated stratum. Otherwise changes of the chemical content of the medium do not seem to be of great importance in determining the vertical movements of *Daphnia*.

VERTICAL MOVEMENTS CAUSED BY AGING OF INDIVIDUALS

Although no careful study has been made of the reactions of any age of the daphnids except the adults, it can easily be observed that the young daphnids show marked differences in behavior from the behavior of the adults. In general the young are more strongly positively phototactic and more strongly negatively geotactic than the adults. They sink less rapidly through the water than the adults. All these features tend to cause the young daphnids to be found on the average nearer the surface than the adults. In many cases the adults reach the surface at some time in the day and in winter they may remain near the surface all day, but in general the adults are found at deeper levels than the young. In the life of the individual there must then be a movement of the average daily position downward through the water until death occurs and the dead body sinks to the bottom. In lakes where the lower levels are stagnant the daphnids will likely be killed soon after they drop below the thermocline.

Reproduction seems to occur in periods. Birge (1897), in Lake Mendota, found one period in the fall and several in the spring. During a period of reproduction young daphnids appear in great numbers and crowd toward the surface. Being in much greater numbers than the adults the percentages of distribution indicates an upward movement of the species. As the individuals grow older they tend to drop into lower levels, and through natural mortality grow few in number.

We must, then, distinguish a periodicity in vertical distribution due to the aging of individuals and the occurrence of reproductive periods.

GENERAL FEATURES OF BEHAVIOR IN *DAPHNIA*

After a considerable study of these daphnids the conclusion is forced on one that they do not behave in a perfectly mechanical manner. They are not little machines which will respond in a definite way each time a definite change is made in the environment. A glance at almost any of the tables included in this paper will make it clear that although there is a tendency to a definite kind of behavior when any particular one of the environmental factors is altered, yet a small proportion of the animals will not react in that particular way, but may even react in a manner directly contrary to the behavior of the majority. It may be that with more exact and thoroughgoing methods of research many of the apparent exceptions could be shown to be due to normal processes. At present the best we can do is to say that environmental changes tend to produce changes in the condition of the animal and that it then reacts differently than before.

In this paper it has been the aim to show the normal tendencies in behavior when a single factor is varied and the others kept constant or eliminated as not contributing to the results. When possible a number of animals were used in the same experiment so that quantitative results were secured. Where this was not possible the results have been checked by a number of repetitions of the experiment or by other methods of control.

In cases where several environmental factors vary at the same time the behavior becomes quite complex and it is difficult to determine in such cases which factor is the more potent and what the resultant behavior will be.

In the previous part of this paper much use has been made of such terms as phototaxis, geotaxis, etc. It is not intended by the use of such expressions to subscribe to any particular theory as to the basis of animal behavior. By the use of these terms it is intended only to express the tendency to move toward or from a source of stimulation. Whether this is due to a tropism caused by unequal stimulation on the two sides of a bilaterally symmetrical organism, or whether the orientation to the stimulus results from the action of trial and error need not concern us here.

It seems that most of the behavior of *Daphnia* is determined by orientation of the body to different sources of stimulation. However, the random movements which occur on exposure to strong light, great cold, or great heat give a means of escape from unfavorable conditions, but secure this result without a definite orientation of the body.

It may be observed that while many of the previously given experiments show tendencies to upward movement it is very seldom that all the animals go to the upper part of the dish. In the experiments showing a tendency to go toward the bottom this tendency is likely to be very strongly marked. It might be argued, then, that the upward movement is not due to a negative geotaxis, but is merely an irregular wandering which naturally would carry many of the animals toward the surface when the factors holding them down were no longer operative. However, it may be observed in many cases, particularly on shading a tall jar of daphnids exposed in sunlight, that there is an immediate and vigorous upward movement. The failure of some to move to the top when the tendency is in that direction must be due in part to the weight of the body, which has a constant tendency to drag the animal down. It is probably also due in part to the unnatural conditions under which the animals were kept. It was observed that daphnids freshly collected from natural ponds showed a greater tendency to upward movement than those kept for a long time in the laboratory. There is the further fact that the jars used for experimentation have a very slight depth in comparison with the average depth of a lake so that the available range of movement was very small. In nature the daphnids do not go to the very surface of the water or they would be caught on the surface film.

The reactions of the animals in moving upward or downward in response to changes in light intensity or temperature might be considered to be due to a change in the reaction of the organism to pressure rather than to gravity. It can be observed that daphnids under constant conditions maintain themselves at nearly a definite height in the aquarium. They may sink several centimeters, but usually soon regain the former position by a few rapid strokes of the antennae. Birge (1897) seems to be of the opinion that change of pressure is the controlling factor in this case. It seems that the differences in water pressure on the upper and lower parts of a daphnid must be very small in amount, and that these differences can hardly act as a directive force in the vertical movements. However, careful experimentation is needed to settle this point.

Although every care was taken to experiment on the animals under as nearly natural conditions as possible, it was not possible to reproduce the conditions of the natural habitat and still be able to control the factors for experimentation. The unnatural conditions in the experiments may have altered the behavior to some extent, but it is believed that the general features of daphnid behavior are as have been indicated.

Daphnia pulex shows a strong tendency to avoid any solid objects, such as the sides of the dish. This indicates that is is a true plankton animal.

When a daphnid is approached by a glass rod or other solid object held in the hand there usually ensues a vigorous movement away from the source of stimulation. This reaction must be of great value to the animals in escaping enemies.

When any considerable change is made in the environment, such as changing the animals to water to which they are not accustomed, or by strong heating or cooling, there is a tendency for a great number to get caught on the surface film. Once caught on this film the animals are seldom able to escape but remain there until they are exhausted and die.

The behavior of *Daphnia pulex* is regulatory in general. Continued exposure to temperatures much above 25° C. produces feebleness or death in these animals. However, in nature such strong stimulation would produce positive geotaxis and perhaps negative phototaxis which would cause the animals to descend to lower levels in the lake wehre the temperature would be lower. Under ordinary conditions the animals remain near the surface where they find food and the normal conditions of existence.

One particular case of very peculiar behavior may be mentioned. A number of individuals of *Daphnia pulex* collected from a small pond on the morning of February 5th showed very strong positive phototaxis in sunlight. As a further abnormality these individuals showed the peculiarity of changing temporarily from positive to negative phototaxis when the light intensity was reduced by shading the dish.

Very likely other factors besides those considered will be found to be operative in affecting the vertical movements of *Daphnia*, but it seems likely that the more important factors have been mentioned.

REVERSAL OF GEOTAXIS IN OTHER PLANKTON ANIMALS

Reversal of geotaxis by changes in light and temperature similar to that found in *Daphnia pulex* has been observed by previous authors in several different groups of plankton animals. A brief reference will be made to some of these observations.

Esterly (1907) found that the females of *Cyclops albidus* were positively geotactic in daylight, but were negatively geotactic in darkness.

It was observed by McGinnis (1911) that *Branchippus serratus* is positively geotactic in light and negatively geotactic in darkness.

An increase of light makes *Balanus* larvae positively geotactic, while a decrease of light makes them negatively geotactic (Ewald, 1912). After a certain exposure to light of any intensity they assume a general distribution in respect to gravity.

The phantom larvae of *Corethra* become positively geotactic in sunlight or strong electric light (Harper, 1907).

Macropsis, a plankton schizopod of the family Mysididae, is always positively phototacitc, but in light from above the animals remain at the bottom of the vessel (Bauer, 1908). Perhaps it will be possible to show that this behavior is due to light causing a positive geotaxis which is more potent than the positive phototaxis.

Loeb (1893) states that *Polygordius* larvae may be made negatively phototactic by heating or by intense light, and that the geotaxis is always positive when the phototaxis is negative and negative when the phototaxis is positive. No such correlation as this is found in *Daphnia pulex*.

Massart (1891) found that the geotaxis of *Chromulina woroniniana*, a spirillum, is positive at temperatures of from 5° to

7° C., while it is negative at from 15° to 20° C. These organisms are found on the surface in summer, but in winter they gather at the bottom of the body of water in which they occur. The relation of temperature to geotaxis in this case is the reverse of the relation found to occur in the other cases mentioned above.

These observations on plankton organisms of several distinct orders and classes go to show that reversal of geotaxis through the agency of changes in light and temperature is a rather widespread phenomenon. The importance of such a reversal of geotaxis in determining the vertical movements of plankton animals must be very great.

SUMMARY

In the experimental part of this paper it has been shown that the individuals of *Daphnia pulex* are normally positive to weak light at a temperature of 20° C. At that temperature they are normally indifferent to light intensities stronger than weak diffuse daylight.

Increase of temperature has a tendency to decrease the positive phototaxis, while decrease of temperature tends to make the animals more strongly positive. At temperatures below 12° C. they are positive to all light intensities.

Increase of light intensity causes a tendency to positive geotaxis, while decrease of intensity causes a tendency to negative geotaxis. These tendencies seem to persist for at least a considerable period of time.

High temperatures produce a tendency to positive geotaxis, while low temperatures cause a tendency to negative geotaxis. These tendencies seem to be very persistent.

The diurnal movements of *Daphnia pulex* are caused chiefly by variations in geotaxis induced by changes in light intensity. The limits of the diurnal movement are determined by the factors effective in producing the seasonal movements.

Change in geotaxis caused by changes in the temperature of the lake at different seasons of the year is the principal factor determining the seasonal movements of this species. The effects of the changes in temperature on phototaxis, and of the seasonal changes in the midday light intensities on geotaxis and on phototaxis are minor factors in this movement.

Strong wave action may cause a temporary inhibition of locomotor activity and this allows the animals to sink to lower levels.

No definite vertical movement due to changes in the chemical content of the water, or to the action of a diurnal rhythm, independent of the effect of recurrent external physical changes, could be found.

Young individuals are more strongly positively phototactic and negatively geotactic than adults. They also sink less rapidly in water. For these reasons they are usually found nearer the surface than the adults. There is a downward movement due to the aging of the individuals.

Much of the behavior of *Daphnia* is determined by orientation to various stimuli, but some regulatory behavior is obtained by means of random movements.

Change in geotaxis by changes in light intensity and in temperature has been observed in other plankton organisms, and is probably of widespread importance in determining the vertical movements of the plankton.

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STUDIES ON THE PHYSIOLOGY OF REPRODUCTION IN THE DOMESTIC FOWL. VII. DATA REGARDING THE BROODING INSTINCT IN ITS RELATION TO EGG PRODUCTION [1]

RAYMOND PEARL

INTRODUCTION

The extensive poultry plant maintained by the Maine Agricultural Experiment Station for experimental purposes offers an exceptional opportunity for the study of the habits, instincts, and behavior in general of the domestic fowl. While hens have been kept under domestication for a very long time, comparatively little systematic study of their adult behavior has ever been made. A splendid field of work is open here for the student of animal behavior. The writer and his associates are collecting data in certain directions within this field. Particular attention is being paid to those features of behavior which have to do with the processes of reproduction. It is the purpose of this paper to present a part of the material which has been collected regarding the brooding instinct in the hen. This material in part illustrates some facts which have not, so far as the writer is aware, hitherto been brought specifically to the attention of workers in animal behavior, and in part, it is believed, brings to light some new facts. This paper is in no way to be regarded as an exhaustive treatise of the subject of broodiness. Certain of the problems involved demand an extensive and detailed statistical treatment and our data on these are left for discussion at another time.

The brooding instinct belongs in the category of what Herrick (3) has well called "cyclical instincts." This author has pointed out that primitively the following cycle of events appears in the reproductive activity of birds: "(1) Spring migration; (2) courtship and mating (often attended by song); (3) selection of nesting site and building nest (often accompanied by fighting instinct); (4) egg-laying; (5) incubation—including care of eggs such as shielding, rolling, cleaning and covering (fear often completely blocked by brooding instinct); (6) care of young in nest ———; (7) care and incidental education of young when out of nest; guarding, feeding, play and other instinctive acts; (8) fall migration." In the domestic fowl, in spite of its long domestication and sophistication in regard to such unnatural things as trapnests and the like, all the instinctive acts enumerated in this list, with the exception of its first and last alone, occur with greater or less degrees of complexity and precision. Even such matters as sexual selection (preferential or assortive mating) and nest building, which domestication might be supposed to have done away with long since, may be observed in the poultry house and yard under proper conditions. We are, however, at present concerned only with five in the series, that is, the instinct for incubating the eggs, or of brooding.

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[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 65.

Herrick (*loc. cit.*) further says: "Beginning at 2, 3, or 4, according to circumstances, the cycle may be repeated once or oftener within the season." In another paper the same author (4) discusses a number of interesting cases of repetition and blending of the different members in this series of cyclical instincts. In certain of the domestic races of poultry, the repetition of the part of the cycle involving at least items 3, 4 and 5 within one season is of such frequent occurrence as to be regarded as a more or less normal condition. Whether or not the same is true of the wild species of *Gallus* it is impossible to say with certainty. Apparently no systematic study of the mating and breeding behavior of the wild *Gallus* has ever been made. The information to be gained from casual notes of travelers or hunters is meager and indefinite. Tegetmeier (9) in a discussion of the habits of the jungle fowl quotes from a "well-known Indian ornithologist who has published the results of his observations in *The Field* under the signature of Ornithognomon" to the following effect (*loc. cit.* pp. 259–260): "The period for incubation varies according to locality, but is generally at the beginning of the rains—i.e., June. I have seen eggs, however, in March, and Jerdon says the hen breeds as early as in January and as late as July. She selects for this purpose some secret thicket in the most retired and dense part of the jungle, scraping together a few leaves on the ground by way of nest. She remains as part of the cock's seraglio until some seven or ten or a dozen eggs have been deposited in the above spot, to which she stealthily repairs every day, and finally quits her party and retires alone and unseen to perform the duties of incubation."

In the case of the domestic fowl it has long been known that the brooding instinct could be aborted by proper treatment. This is obviously an important matter when hens are kept for egg production. Since a hen lays no eggs while broody the sooner the desire to " sit " can be overcome the sooner will she be brought back to the profitable performance of her duty as an egg producer. The usual method adopted for overcoming the tendency to brood is to confine the bird in a small coop with a slatted or bare board floor. Usually in a comparatively short time the tendency towards broodiness will disappear and if the bird is then put back under normal conditions she will again commence to lay, and may continue to do so for some time before the onset of another spell of broodiness. Just why this treatment should be so effective as it actually is, is not entirely clear. Formerly it was supposed to be necessary to " cool the blood " in order to " break up a sitter," and the somewhat drastic treatment of dipping the bird in a bucket of ice water was practised. It is probable that the chief factors concerned in producing the good results following confinement in a small coop are (1) that the bare floor and absence of eggs gives no encouragement to the bird to " sit," but on the contrary acts as a set of stimuli strongly antagonistic to this phase of instinctive behavior and (2) that the sudden change of conditions acts to upset the more or less delicately balanced physiological and psychical condition which characterizes the broody bird.

The instinct of brooding varies greatly in different breeds of domestic poultry. Some breeds—notably those classed by poultrymen as Mediterranean—have the instinct very slightly developed. Others—for example certain of the Asiatic breeds—go to the other extreme and have the instinct very strongly developed. The so-called American breeds, on the whole, occupy an intermediate position in this regard. With them the usual or normal course of events relative to broodiness is as follows:

1. During the winter months a number of eggs are laid. This constitutes what may be considered a first clutch.

2. Sometime in the early spring the hen stops laying and becomes broody. If she is not allowed to incubate eggs the broodiness disappears after a varying length of time depending on circumstances.

3. She lays another clutch of eggs, and

4. Becomes broody again, and so on.

This sequence of events—a period of laying followed by a period of brooding—may be repeated several times over. Usually after early summer the tendency to broodiness becomes greatly diminished or disappears altogether.

It will be seen that this series of events is very similar to a repeated cyclical instinct in wild birds. The normal sequence is broken into at the brooding stage by the fact that the hen is not allowed to incubate. She then begins anew at the next preceding phase of the cycle, viz., egg-laying. Now while this sequence of events is undoubtedly to be regarded as the normal one for so-called " broody " breeds of domestic poultry, there are numberless variations from it in individual cases. In this paper some of these variations will be described and discussed.

It should be noted that the behavior ordinarily classed by the poultryman inclusively as " broodiness " really belongs in two rather distinct categories. In the first place there is (a) the instinct to sit upon and incubate eggs. This is in many respects an altogether different thing than (b) the instinct to " brood " a flock of little chicks after they are hatched. The two forms of behavior are of course closely related to one another, and objectively have a number of features in common. But there are also marked differences. It is important to emphasize at this point that the present paper has to do entirely with the first of these instincts, namely that of incubation. In accordance with general usage, I have employed the terms "broodiness," "broody," etc., to designate this instinct. I desire, however, to make perfectly clear the restricted sense in which the terms are here used.

THE NATURE AND METHOD OF COLLECTION OF THE DATA

In the poultry work of this Station the only sort of nests provided for the laying birds are trap nests. Consequently, with the exception of an occasional egg laid on the floor (*Cf.* Pearl [5]), a record is obtained of every egg laid and of the hen which laid it. It is further the practice to confine birds which are broody in small coops until the particular manifestation of the instinct shall have disappeared. Beginning in December, 1907, and continuing until the present time, the practice has been followed of making a record of the date on which any bird is put into confinement for broodiness, and also of the date on which she is released from confinement as "cured." These records were made by putting "B" in the space corresponding to the date of onset of broodiness and "O" in the space corresponding to the date of release, on the poultry house egg record sheets. Records so obtained form the material of this paper. The records here discussed came, in the main, from 850 Barred Plymouth Rock pullets hatched in the spring of 1907. This breed will alone be considered in this paper.

In a critical consideration of these data the question at once arises as to their accuracy. Does the instinct of brooding manifest itself with such clearness that the recorded date of onset corresponds substantially with the actual? And further, to what extent does the date of release measure the actual subsidence of the instinct? These questions may be considered in order. The onset of a period of broodiness is, *at a certain stage*, marked by a characteristic behavior which is immediately and certainly recognizable by an experienced poultryman. Whether the stage at which this characteristic behavior begins marks the absolute beginning of the physiological state which underlies the instinct of broodiness is a question impossible of answer and really of no particular significance from the present standpoint. This behavior is the objective criterion of broodiness. Whatever preliminary internal or subjective stages the bird may go through leading up to this objective behavior constitutes a field of inquiry separate from the study of the behavior itself. This leads to the question as to whether the behavior connected with the onset of broodiness is so characteristic as to be easily and certainly recognizable. Of this there can be no doubt. The following characteristics are perfectly definite and obvious.

1. Continued sitting on the nest. As soon as she is thrown off the nest, the "broody," in the early stages, promptly returns.
2. A peculiar "clucking" note, not made by the bird at any other time in her life.

3. A raising of the feathers over the whole body, giving the bird a ruffled and very much enlarged appearance.
4. A marked pugnacity of behavior when anything approaches the sitting bird.

This brief statement gives an idea of the criteria of broodiness used in actual practice by the poultryman. When a bird exhibited these symptoms in a characteristic manner, she was confined and a " B " entered on the record. The records of *onset* of broodiness discussed in this paper can be unreservedly accepted as accurate and complete.

Turning to the " O " or release records, the case is somewhat different. A bird is in practice released from the detention coop when she no longer exhibits the symptoms of broodiness but instead appears normal in her behavior. Now since, as a matter of fact, there is not a sudden disappearance of the manifestation of broodiness following confinement, but instead a gradual subsidence of the symptoms, it must be clear that the time when a bird shall be released is an extremely difficult matter to decide. And further, records of the dates of release do not possess anything like so precise a metric significance as do dates of incarceration, so far as the manifestations of the instinct of brooding are concerned. The observer will frequently make the mistake of releasing a bird too soon and there will be an immediate recrudescence of the broodiness under the conditions of freedom, necessitating a second confinement. Or again, there is reason to suppose that sometimes the birds are kept in confinement too long. Evidence of this is given in cases where the bird lays on the same day that she is released. All that can be said regarding the release records is that every care was taken to make them as accurate and significant (i.e., in relation to the cessation of the manifestation of broodiness) as possible. From the nature of the case, however, they are not and cannot be *precise* records. This means that a great deal of caution must be exercised in drawing conclusions from them, and each individual case must be considered critically.

With these statements as to the character of the data in hand, attention may be turned to some actual records selected to bring out the following points:

1. Broodiness as a cyclical instinct.

2. Recurrence of brooding instinct with different degrees of intensity in the same hen.

3. Occurrence of brooding instinct outside of the breeding or mating season.

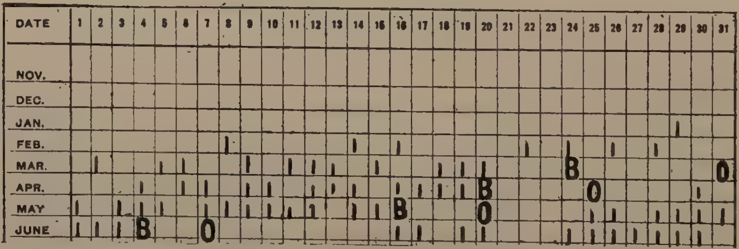
4. Broodiness not preceded by egg laying, or by very little egg laying.

5. The brooding instinct manifested with a very slight degree of intensity.

It should be said that all records of broodiness are exhibited in the form of tables giving the daily egg records of the birds. A single vertical stroke in the space corresponding to any given date signifies that on that date the bird which is the subject of the record laid an egg, while a blank space denotes the confinement of the bird on that date because she showed the characteristic symptoms of broodiness. An " O " signifies that the bird was released from confinement " cured " on the date indicated.

BROODINESS AS A CYCLICAL INSTINCT

It has been pointed out above that the normal course of events respecting broodiness in domesticated poultry is to be regarded as a sequence of egg-laying periods and periods of brooding. Table 1 embodies a record showing in a very clear and somewhat extreme form the instinct of brooding occurring in this cyclical fashion.



DATE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
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FIGURE 1. Egg record of bird No. 139.

From this figure it is seen that in bird No. 139 the first appearance of broodiness was on March 24, following the laying of 19 eggs. On the eleventh day following—seven of these days having been spent in the detention coop—she began laying again. After laying 12 eggs she became broody again on April

20. On the tenth day following laying was again resumed and 13 eggs were laid before broodiness again appeared on May 16. On the ninth day following laying was resumed and 9 eggs were laid before the appearance of the last recorded period of broodiness beginning June 4. In this record the regular periodicity in the recurrence of the brooding instinct, particularly as measured by the number of eggs laid in the intervening "clutches," is striking. It will further be noted that in no case is the duration of the "broody" period, as measured by the number of days intervening between the laying of the last egg in one "clutch" and the first egg in the next, even approximately as great as the normal period of incubation of the hen's egg, 21 days. The treatment by confinement aborts the brooding instinct. Another point worthy of note is that the date of release, which indicates the disappearance of visible symptoms of broodiness, in each case precedes the date of beginning of the next "clutch" by some days.

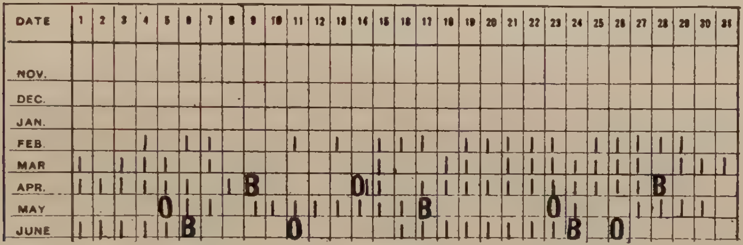

FIGURE 2. Egg record of bird No. 75.

Another record of the same general type as the last, but involving some different features is shown in Fig. 2.

This record shows the occurrence of 5 periods of broodiness with intervening "clutches" of 13, 10, 10 and 8 eggs. The first period of broodiness occurred in the height of the breeding season (April 9) and the instinct was evidently asserting itself at this time with slight intensity. This is indicated by the fact that only 4 days intervened between incarceration and release, and that even then an egg was laid on the day of release. In the later periods of broodiness the instinct apparently became progressively more intense.

As a final illustration of the typical cyclical appearance of broodiness the records of hen No. 251, as shown in Fig. 3, may be examined.

In all essential particulars this record is very much like that of hen No. 75 given in Fig. 1. Here the first onset of broodiness was on April 8. After 8 days laying began again; 14 eggs were laid; the second attack of broodiness began May 1. After 10 days laying was once more resumed and again 14 eggs were laid before the brooding instinct made its appearance. Laying began after 9 days and this time 72 eggs were laid. The next period of brooding occupied 9 days (i.e., between laying dates). This case is noteworthy for the evenness of the " clutches " and of the intervening brooding period.

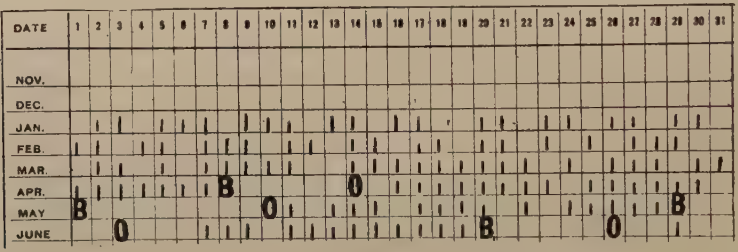

FIGURE 3. Egg record of bird No. 251.

RECURRENCE OF BROODING INSTINCT WITH DIFFERENT DEGREES OF INTENSITY IN THE SAME HEN

From an examination of any large collection of egg record statistics in which broodiness is recorded it will be found that there occur not infrequently individuals in which the instinct to brood is manifested with different degrees of severity at different times, indicating a similar variability in its underlying physiological basis.

An example of this phenomenon is shown in Fig. 4, which gives the record from November 1 to July 1 of bird No. 4.

Here it will be seen that the first period of broodiness began on March 16 and the hen did not again lay until April 2. After laying 4 eggs, she again became broody on April 8, but the period did not last as long as the one before since she was released on April 18 and was laying on the 19th. She did not again become broody until June 14 and this period lasted only 4 days. The bird was released from confinement on the 18th of June and laid an egg on the same day. In this case we have periods of visible manifestation of the brooding instinct lasting 15 days in one case, 10 days in a second case and 4 days in the third case. This certainly indicates a considerable degree of variability in the manifestation of the instinct.

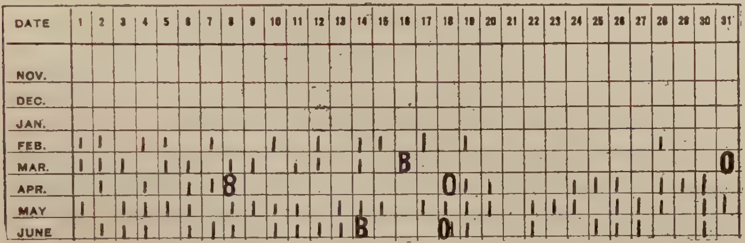

FIGURE 4. Showing the egg record of bird No. 4.

A similar relation is shown in the case of bird No. 444, whose record from November 1 to July 1 is shown in Fig. 5.

This bird was broody at five different times during the period here under consideration. On the first occasion, she was noticed to be broody on January 8, having last laid on January 5. She was released on January 17, but did not lay until February 13, a rest period of 38 days. When she next became broody on March 15, there was an interval without laying of only 13 days.

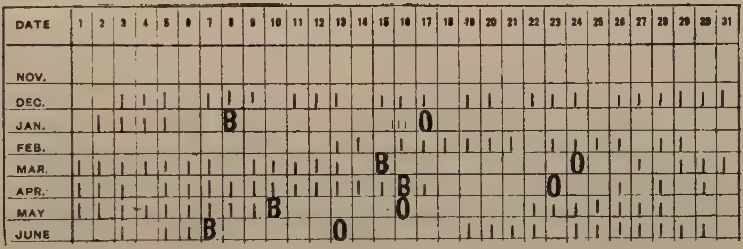

FIGURE 5. Record of bird No. 444.

The rest period of her next broodiness was still shorter. This began on April 16 and lasted but 10 days, on one of which (April 17) the bird laid an egg. The next period of broodiness began May 10. Visible signs lasted 6 days. The whole period during which egg laying stopped was 12 days. Essentially similar relations were shown for the June period of broodiness which began June 7.

These illustrative cases of recurrence of brooding instinct with different degrees of intensity in the same hen could be multiplied many times from our records. There can be no doubt as to the essential fact that the instinct to brood varies in the intensity of its manifestation at different times.

OCCURRENCE OF THE BROODING INSTINCT OUTSIDE OF THE BREEDING OR MATING SEASON

While, as has been seen, broodiness is fundamentally a part of the cyclical series of reproductive phenomena, yet under the more or less artificial conditions of domestication striking changes in its seasonal incidence are frequently to be observed. A hen will go broody at a season of the year when reproduction under normal circumstances would never occur. Furthermore, it often occurs at a much younger age than that at which a bird normally first broods.

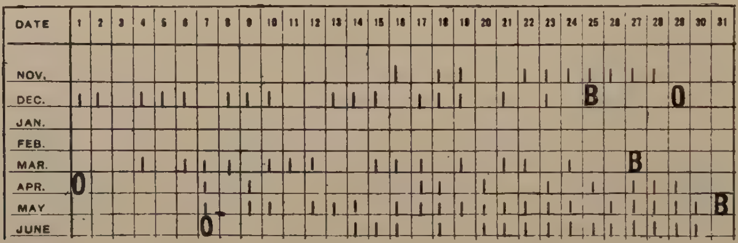

FIGURE 6. Showing record of bird No. 689.

An example of this sort is shown in Fig. 6, which gives the laying record of bird No. 689, from November 1 to July 1.

Here it will be noticed that the bird first became broody on December 25. She did not lay again until March 4 and then again became broody on March 27. It should be said in connection with this record that bird No. 689 was a pullet hatched in the preceding April and was, therefore, at the time when she first went broody roughly eight months old. That this is extremely early for broodiness to occur is shown from general statistics as to the monthly incidence of the first broodiness shown by the individual. During the year for which statistics on this point have been collated there were out of 395 birds which became broody at any time but three that manifested this instinct during the month of December. This is approximately 0.76 per cent. of the flock showing broodiness as early as December. Only 10 of the birds manifested the brooding instinct during the month of January, and 8 in the month of February. Thus all told there were but 21 out of 395, or approximately 5.3 per cent. of the birds which became broody before March 1.

It might be thought that the number of eggs which No. 689 had laid before December 25 was the cause of her going broody at so early a date. As a matter of fact this is not the case because there are many cases (probably hundreds of cases) in our records where pullets laid more eggs than No. 689 during the early winter period and did not go broody at all. A single example may suffice to illustrate the point here. Bird No. 47K laid 106 eggs before February 1 of her pullet year and did not go broody at all. This egg production, it will be seen, is enormously in excess of that of No. 689.

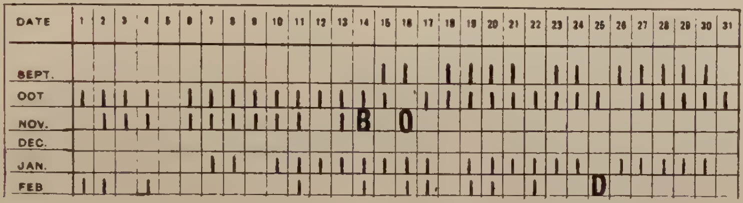

FIGURE 7. Showing the record of bird No. 252-E.

A case of still earlier first broodiness is shown in Fig. 7, which gives the record of bird No. 252E.

This bird was hatched March 31, 1908. She began laying on September 15. She thus began laying when 168 days old. In September she laid 13 eggs, in October 28 eggs, and in November 10 eggs. On November 14 she showed the characteristic behavior of broodiness and was isolated. The symptoms, however, quickly subsided, and she was released on the 16th. The period of rest was protracted until January 7, when she again began laying. She laid through January and less regularly in February up to February 25, on which date she died. In this case the bird first became broody when 228 days old.

Still another case of this sort is shown in the record of bird No. 260E, which is shown in Fig. 8.

This bird was hatched March 31, 1908, and laid her first egg on October 12 at an age of 195 days. In October she laid 13 eggs and in November 7 eggs, going broody on November 9. She was thus at the time of her first broodiness 223 days old. The rest period in this case lasted until December 19, when she began laying again. Before August 1, 1909, at which time she was sold, this bird went broody 6 times, as indicated in Fig. 8. She presents a remarkable record for precocious broodiness, preceded by the laying of only a relatively small number of eggs, namely 20.

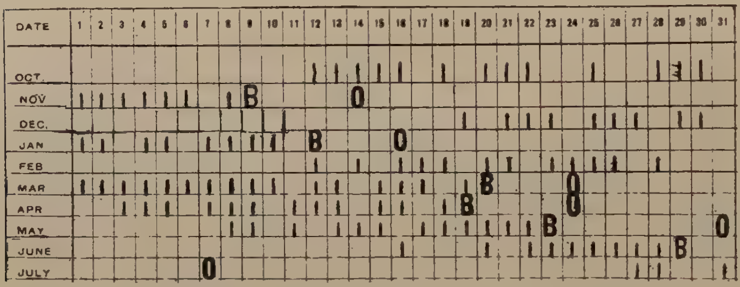

FIGURE 8. Showing the record of bird No. 260-E.

Still a third case of extremely early and frequent broodiness is found in bird No. 380E. This bird was hatched April 15, 1908. She began laying on September 27 at an age of 165 days. She laid fairly continuously, as indicated by the record, up to November 9, when she became broody for the first time. Altogether she produced 29 eggs before November 9. The rest period lasted until January 6, when she began laying again. This bird was only 208 days old at the time of her first broodiness. Like bird No. 260E, she went broody several times in her life; five before August 1, at which time she was sold. This case differs from those already cited chiefly in the fact that the bird was somewhat younger, both when she began to lay and when she first went broody.

BROODINESS NOT PRECEDED BY EGG LAYING OR BY VERY LITTLE EGG LAYING

It was suggested in the preceding section that there was no necessary connection between the number of eggs laid and the manifestation of the brooding instinct. This is very clearly shown by the cases which will be discussed in this section. These are cases in which a bird became broody with little or no antecedent egg production. One of the most striking of such cases in all of our statistics is that shown in Fig. 10, which gives the egg record for bird No. 699 from November 1 to July 1.

It will be seen that this bird went broody on May 10. The only record of egg production before that time is a single egg on November 27. There is every reason to believe that this record of November 27 is an error, probably to be accounted for as an instrumental error of the trap-nest operation. At the time when this record was made the old style trap-nests were in use at this Station. These were in a number of particulars unreliable (cf. for example Pearl [5]). General knowledge of the laws of egg production gained through a number of years study of such matters at this laboratory would indicate with great probability, indeed, practical certainty, that this record was an error. However, if it be allowed to stand, it is clear that it can have had nothing to so with the manifestation of the brooding instinct over five months later. Following this broodiness, bird No. 699 laid an egg on May 29 and another on June 19. These two records are probably correct, since other similar cases are to be found in the Station records. This case proves definitely *that imme-*

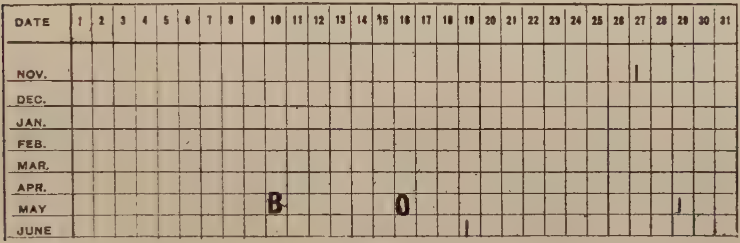

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FIGURE 9. Showing the record of bird No. 699.

diately antecedent laying is not a requisite for the manifestation of the broody instinct.

Similar evidence is afforded by the case of bird No. 130, whose record is given in Fig. 10. This bird became broody on March 16. The records show only one egg before this time to her credit. Whether or not this egg record is an error it is impossible to say. It make no essential difference in the interpretation of the case. Perhaps the most striking feature of this case is the fact that this bird went broody for a second time on April 14, there having been no intervening egg production between the broodiness of March 16 and that of April 14. On May 2 and on May 10 the bird laid an egg. This record essentially confirms the results shown in the case of bird No. 699.

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FIGURE 10. Showing the record of bird No. 130.

The record of bird No. 320 is interesting in this same connection. This record is shown in Fig. 11.

Here there are four distinct and separate manifestations of the brooding instinct between March 25 and July 1. The first period of broodiness began on March 25. Before this time the bird had laid 12 eggs, 11 of them in January and one in March. This egg in March was laid on the 8th and it was 17 days after this before broodiness appeared. It would be extremely difficult to establish any connection between the antecedent laying and the broodiness in this case. On April 19 the bird laid again, this being the first egg since the one of March 8. On April 21 she became broody again, but this was only a mild attack, for she showed visible manifestations on the 24th and laid on the 26th, only to become again broody on the 30th of April. She was released on May 4 and laid May 12 and May 16. The latter of these was her last egg before July 1. Twenty-nine days after this egg was laid, without any intervening production whatever, the bird became broody again on June 14.

The above described observations on normal hens, indicating that the brooding instinct may become manifest without relation to antecedent laying, is supported by experimental work carried on in this laboratory. Such evidence is derived from cases in which the oviduct was completely removed from the bird by a surgical operation, making it impossible for that bird to lay thereafter. Two cases of this sort will be cited here. The protocols of the operations will be given first and then an account of the subsequent behavior of the hens.

Operation No. 34. November 13, 1908. Bird No. 911C. Hatched June 11, 1908. Body weight, 1,480 grams. Under ether anaesthesia[2] the oviduct was completely removed, with the exception of that part of the vagina which is closely attached to the cloacal wall. The left ureter was tied off and cut with the oviduct. All of the ureter, however, was left in the body. The oviduct at the time of the operation was in infantile condition.

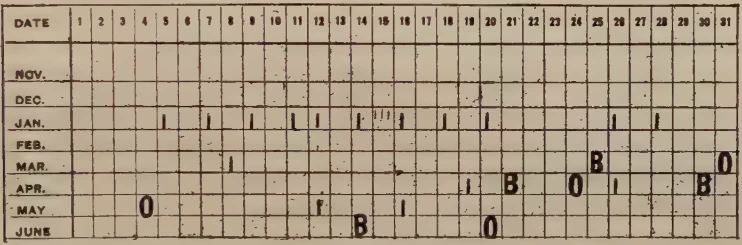

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FIGURE 11. Showing the record of bird No. 320.

This bird made an uneventful recovery from the operation. She died and came to autopsy June 14, 1909, that is, 213 days after the operation. The autopsy record is as follows: The oviduct was found to have been completely removed, with the exception of the vagina, which was closely attached to the cloaca. Left ureter had been cut and ligated. It was very much enlarged and filled with a white mass of urates, etc. Evidently the left kidney had almost entirely atrophied. The portion still remaining was covered with a heavy layer of fat. The right kidney had hypertrophied. Remainder of viscera normal.

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[2] Administered according to the method described by Pearl and Surface (8).

Loose in the body cavity were a number of small irregular shaped hard masses like hardened yolk. These were not enclosed in the peritoneum and showed no decay. Ovary had four or five small absorbing yolks all below one centimeter in diameter. A few small normal yolks (not showing signs of progressing absorption). The body weight at autopsy was 1,995 grams.

While this bird never laid after the operation she frequently went on the trap-nest as though about to lay and was given an "*n*" or nesting record. (Cf. Pearl [6]). On May 28, 1909, this bird showed visible signs of broodiness and was incarcerated. The visible signs of broodiness ceased on June 2 and the bird was released. As has already been stated she died June 14, 1909.

This case demonstrates beyond question that it is not necessary for eggs to be completely separated from the body of the bird (i.e., laid) in order for broodiness to occur. There had, of course, undoubtedly in this case been ovulation into the body cavity from the ovary. This is shown by the fact of record and by the masses of incompletely absorbed yolk found at autopsy.

The second case is of slightly different character, though bringing out the same points. In this operation, the oviduct was not removed but was completely closed near the infundibular end, so that no egg could enter the duct.

The protocol follows.

Operation No. 94. April 16, 1909. Bird No. E490. Barred Plymouth Rock. Body weight 2,220 grams. Under ether anaesthesia the bird was opened. An egg about to be laid was removed from the uterus and a large glass marble was inserted into the oviduct at the mouth of the funnel. The funnel mouth was then completely closed with a series of closely spaced stitches, making it impossible for anything to leave or enter the oviduct at that end. The bird made an uneventful recovery from the operation.

This bird, of course, never laid after the operation, but on July 24 she became broody and continued with visible manifestations until July 27, at which time she was released. Prior to the operation, the bird's laying record had been as follows: In January she laid 2 eggs, in March 13 eggs, in April 6 eggs before the date of operation. She had never been broody before the operation, but, as already stated, did become so on July 24 without any antecedent laying.

A change in the order of events in the cyclical processes of reproduction is well known for other birds. While normally broodiness follows a period of laying, it does not always do so, even in other birds than the domestic fowl. Replying to an inquiry regarding this point in pigeons, the late Professor C. O. Whitman wrote me on October 22, 1909, as follows: " You ask whether in pigeons broodiness ever occurs without the laying of eggs. I have had such cases in different species many times. For example, a pair of Pouters, hatched last year, have repeatedly built a nest this summer without laying any eggs and yet have incubated the empty nest in quite regular order, the male and female alternating in sitting."

Similar disturbances of the normal sequence of events in the reproductive cycle of mammals are not unknown. I might cite here by way of illustration a case of appearance of heat in a mare shortly before parturition (Bell, [1]). He says:

" The thorough-bred mare, Lady Gower, foaled on April 12. The foal was a very small one, and only lived for a short time. During the period of utero-gestation there was nothing to call for remark until March 5th, five weeks before the mare was delivered of the foal. On this date the symptoms of oestrum were most marked, and she was put to the horse, no suspicion being then entertained that she was in foal. What is still more remarkable, however, is the fact of the recurrence of oestrum on April 7 and April 11, on both of which dates the mare was served, parturition taking place the day after the last service."

THE BROODING INSTINCT MANIFESTED WITH A VERY SLIGHT DEGREE OF INTENSITY

It is not infrequently found to be the case, especially with birds which are good layers, that well defined brooding behavior may appear, only to disappear very quickly under the confinement treatment. Such cases indicate that either the original intensity of the instinctive behavior was slight or else it was very quickly aborted.

Records of this kind are shown in Figs. 12 and 13.

Fig. 12 gives the record of bird No. 401 from November to July 1. It will be seen that this bird was a fairly good winter layer. She showed no signs of broodiness until May 6, when she very clearly gave the manifestations of broodiness, and was, on that account, incarcerated. The symptoms, however, quickly subsided. She was released on May 9 and laid an egg the same day.

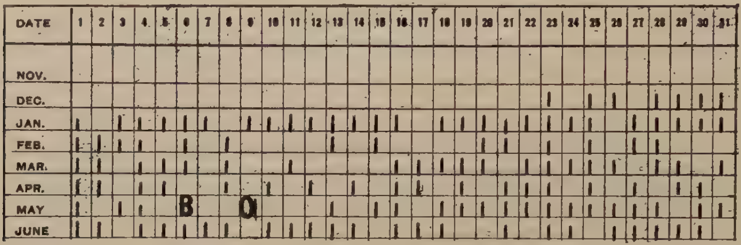

FIGURE 12. Record of bird No. 401.

The record of bird No. 408 almost parallels this, the chief difference being in respect of the time at which broodiness appeared. In the case of No. 408 it was on May 23, and was clean-cut and definite. The manifestations, however, quickly disappeared. On the 27th the bird was released, and laid an egg the same day.

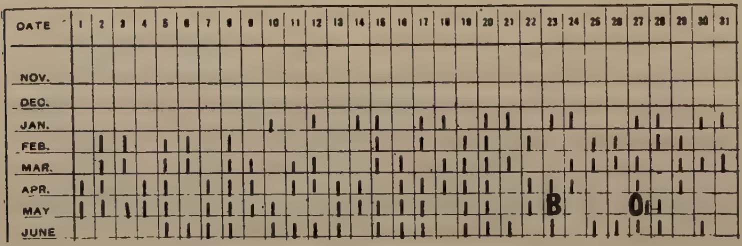

FIGURE 13. Record of bird No. 408.

DISCUSSION

In this paper I have tried to bring together some of the facts regarding broodiness in fowls which appear clearly when one collects extensive and accurate statistics on the matter. The essential purpose of this paper is to define the problems which need further physiological analysis rather than to solve them. The data presented in this paper are facts which any theory of the physiological basis of brooding behavior must take into account.

In the present state of knowledge the physiological cause or basis of the phenomenon known as broodiness, which every bird shows in one form or another, is not at all clear. From the facts set forth in this paper it is obvious that broodiness is a much more variable phenomenon than oestrus in mammals. In the first place it lacks entirely the regularity of the occurrence of oestrus. Even in the cases where periods of broodiness do recur rather regularly (cf. Figs. 1, 2, and 3) it is clear that we have nothing like the regularity of the dioestrous cycle of mammals.

It is furthermore certain that brooding is not a necessary or essential element in the reproductive processes in the domestic fowl, in the sense that any other element in the cycle is dependent upon it as a necessary antecedent. Some hens which lay perfectly well throughout their lives, and whose eggs produce perfectly normal healthy chickens never manifest the slightest indication of the brooding instinct.

It appears to be the case that in the domestic fowl the brooding instinct has to a very large degree disappeared along with the fact of domestication. This is particularly true in the case of fowls which have been systematically bred for a considerable period of time for high egg production. In such strains it is difficult to find fowls in which the brooding instinct is sufficiently strong to last out the 21 days necessary to hatch eggs. Here we have repeatedly tried during the last six years to get broody Barred Plymouth Rock hens to hatch eggs. Only in extremely few cases has it been possible to do this. In most cases the bird will sit for a while, then cease all manifestations of the instinct and begin laying again. It seems highly probable that broodiness is in some way dependent upon factors which are inherited in a Mendelian manner. A large amount of material has been accumulated regarding this point and it is hoped that the analysis of it will soon be completed.

It would seem that broodiness is rather directly connected physiologically with the functioning of the ovary. That it is not connected with the functioning of the oviduct is clearly demonstrated in the present paper by the cases in which the oviduct is removed, or put into a non-functioning condition. In these cases, however, the normal functioning of the ovary had in no wise been interfered with. It is an interesting fact in this connection to note that birds in which the ovary is non-functional never show manifestations of broodiness. Evidence on this point is found in cases of incomplete hermaphroditism such as that described by Pearl and Curtis (7). In the case referred to, the bird, No. 16D, had a non-functional ovary. Her record shows that she never manifested the slightest signs of broodiness. Still more striking evidence is afforded by the case of bird No. 8051, which was described by Pearl (6). This bird had an ovary which was apparently entirely normal, but remained throughout life in an infantile condition. This bird was hatched on March 29, 1909, and died August 24, 1912. During the whole life she never visited the nest, or showed in any way the slightest manifestations of broodiness. A photograph of the ovary of this bird is given in the paper cited. This is apparently a case of a normal but non-functional ovary and no broodiness occurred.

Interesting light has recently been thrown on the question of the physiological condition of a brooding bird by the very thorough and extensive investigation of Gerhartz (2). This author shows that the state of broodiness is one of profound physiological rest or depression. He says: (*loc. cit.* p. 44).

"Der Netto-Energieverbrauch für die auf dem Nest sitzende Bruthenne ist ausserordentlich niedrig: 53.4 Cal. pro Kilogramm Korpergewicht und Tag. In derselben Periode liegt der Energieverbrauch bei der night sitzenden, aber sich doch sehr ruhig verhaltenden Henne ebenfalls sehr niedrig: bei 74 Cal. Geht man von dem erstgenannten Minimalwert aus, so zeigt sich, dass der Energieverbrauch beim Huhn, das in normaler Ruhe ist und sich in einem geraumigen Käfig aufhalt, im allgemeinen um 59.5% des Minimalwertes höher liegt (Plus von 31.73 Cal. pro Kilogramm und Tag), in der Mauserperiode aber gar der pro Kilogramm und Tag erforderliche Energiebetrag um 84% des Minimal wertes steigt, also fast den doppelten Wert erreicht. In der Legeperiode erhoht sich der Bedarf um fast das Dreifache."

This discovery that the brooding state is one of physiological depression is somewhat contrary to the common belief of poultrymen, who have usually supposed that broodiness indicated a condition of unusual physiological excitation. The precise measurements of energy metabolism which Gerhartz has given are, however, conclusive. It is not clear, from the behavior standpoint, what the relation is between the manifestations of the brooding instinct, and the physiological state of the bird. In this connection it may be noted that it frequently happens that a bird will exhibit periods of rest in egg production, which are as long continued as those of broodiness, and yet show none of the objective features of broodiness whatsoever. Such cases prove that the cessation of ovarian activity (laying) is not *alone* capable of causing the onset of broodiness. It would be extremely interesting to have more extensive data as to energy consumption in these birds which are not laying, and yet are not manifesting the broodiness instinct.

In the fowl, broodiness seems to be distinctly a female secondary sexual character. This, of course, is not true in some other species of birds where the male bird alternates with the female in brooding eggs. Ordinarily in the domestic fowl the cock takes no part whatever in the brooding of the eggs or the chicks. It has, however, long been the practice with practical poultry keepers in certain parts of the world to use the castrated cock or capon for the purpose of brooding chickens. I know of no record of capons being used to incubate eggs. The brooding behavior of the capon needs, and will certainly repay, careful study by a trained behaviorist.

SUMMARY

This paper presents data regarding variations in the manifestations of the brooding instinct in fowls. It is shown that:

1. Broodiness normally constitutes one element in the cyclical reproductive activities of the female. It recurs with greater or less regularity following periods of laying.
2. The degree of intensity of the brooding instinct, both in respect of its objective manifestations and in respect of its physiological basis, may vary considerably at different times in the life of the same individual.
3. Broodiness in the domestic fowl is not necessarily connected with any particular season. It may occur entirely outside the regular breeding season.
4. While ordinarily broodiness is preceded by the laying of a " clutch " of eggs, this need not necessarily be so. Cases are cited in which well marked broodiness occurs without antecedent laying.

5. Well marked broodiness behavior may in certain cases disappear very quickly.

6. The manifestations of the brooding instinct are apparently closely connected with the functional activity of the ovary, though the precise nature of the connection has not yet been analyzed.

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NOTES

ON THE THELE-PERCEPTION OF SEX IN SILKWORM MOTHS

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While carrying on a series of researches on the caterpillar of *Bombyx mori* L.,[1] my attention was attracted by a phenomenon presented by the male moth just after emerging from the cocoon. The moth began to move its wings very rapidly while clinging with its feet to some one of the still unopened cocoons, and it remained thus even after the moth from that cocoon had emerged. It occurred to me that this might be due to the fact that the unopened cocoon held a female, to which the male was guided by some peculiar scent. After postponing for several years any attempt to prove the truth of this supposition, I have at last made some systematic observations which are here recorded.

It has long been noticed by naturalists that the male moths of the Bombicidae, immediately on emerging from the cocoon, seek out the female, guided, it is supposed, by the sense of smell. The wings of the female are not well developed, and they seldom fly far; the males, on the other hand, may make real migrations in search of the female.

It is also well known that certain moths emanate peculiar odors. The seat of the odor was shown by Fritz Müller[2] to be small blades provided with a gland at the base, situated in the superior part of the anterior wings near the junction with the thorax. To these he gave the name "Andraconia." He described the odors of a large number of moths and butterflies, some of which were pleasant and others disagreeable. Müller considered these odors a means of sex attraction. Leoni, however, found them present in both males and females and interpreted them as a means of recognition among individuals of the same species.

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[1] Polimanti, O. Contributi alla fisiologia del` baco da seta (*Bombex mori*) Scansano. Tessitori. 1906. Contributions à la physiologie de la larve du ver a soie (*Bombyx mori*). *Archives italiennes de biologie.* T. **47.** 1907. P. 341-372.

[2] Müller, Fritz. 1. Wo hat der Moschusduft der Schwärmer seinen Sitz? Kosmos. 1878. 2 v. 3. p. 84. 2. Duftbüschel von Sphingiden. *Transactions Entomological Society,* London. 1878. P. 2.

Fabre[3] carried on some experiments, to determine this point, with *Saturnia pyri* and *Gastropacha quercus.* He placed a female of Saturnia in a cage of wire netting. During the night the cage was surrounded by males of the same species. To ascertain whether it was by means of the antennae that the odor was perceived by the males, he cut off their antennae and moved the female to another room. On the following night only one of these males with amputated antennae was found in the number which flocked around the cage. This fact might be due, however, to the short life of the adult male. In all, Fabre captured, during eight evenings, one hundred and fifty males, which was the more remarkable because very few individuals of this species had been known in that vicinity, and very few cocoons had been found. Some of the moths must have come long distances. Fabre explained the phenomenon by the existence of emanations insensible for us but capable of influencing an olfactory sense more acute than ours. He experimented also with receptacles, for the female, of different materials, of tin, wood and pasteboard, and found that only when these were hermetically sealed did the males fail to find the female. Nor did the attempt to mask the odor by means of other strong odors, like those of naptha, essence of nard, petroleum, carbon disulphide, have any different result. When the female was placed under a glass shade, the males paid no attention to her, but hovered around the cage in which she had previously been confined. In this last experiment, it became evident that sight had nothing to do with attracting the males. These experiments were repeated later by Fabre with Bombyx.

The experiment of cutting off the antennae of the oak eggar (*Gastropacha quercus*) gave doubtful results. The grass eggar (*G. trefolii*) showed less acuteness in discovering the female. The existence of a special odor in the female of Saturnia and *Gastropacha quercus* was, however, thoroughly established by Fabre's experiments. How these odors are perceived remains to be solved. It is difficult to imagine any substance which, according to physical and physiological laws, could be so diffused as to be perceptible at a distance of many kilometers; and just as extraordinary must be the sense which serves to discover it. Fabre is right in observing that the world of sensations is much wider than our imperfect and obtuse organs of sense reveal to us. It is now certain that animals, for instance, hear sounds that escape our ears; see ultra-violet rays which our eyes do not see. It is easy to believe that these lower organisms, especially the insects, are endowed with organs of sense quite special and so complicated that they differ absolutely from ours. They may serve purposes as different from any of ours as sound, for instance, differs from light. It is only by indirect methods, that is, by the study of ethology, of the intelligence of animals, of their relation to the forces of nature, of the appearance which the external world has for them, that we can arrive at the discovery of the senses and sensations which are now only an hypothesis.

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[3] Fabre, J. H. Souvenirs entomologiques. Paris. T. 4. P. 56.

Another characteristic of the *Bombyx mori* which I studied, and also of other moths, is the buzzing made by the wings. In the males of Bombyx, this is more intense than in the females, and the movements of the wings are more rapid. The movements are more rapid also when the male is resting upon a cocoon which contains a female moth about to emerge, than when it rests upon any other object. In this case, the male may hear the movements of the female inside the cocoon, and having thele-perception of the sex, augments the vibrations of his wings.

In performing my experiments, I took two hundred cocoons of *Bombyx mori* and kept them in a big pasteboard box at a constant temperature of 15° C. As the moths emerged, I recorded whether they attached themselves at once to another cocoon, whether they remained there constantly until the enclosed moth came out, and whether the latter was of the same or different sex. I reckoned also the uncertain results, that is, the cases where the moth did not remain constantly on one cocoon, but went to another from which afterwards came a moth of the same or different sex.

TABLE

SUMMARY OF EXPERIMENTS

No. of moths ♂ attached to cocoons from which came moths ♀ and quantity %	No. of moths ♂ attached to cocoons from which came moths ♂ and quantity %	No. of moths ♀ attached to cocoons from which came moths ♂ and quantity %	No. of moths ♀ attached to cocoons from which came moths ♀ and quantity %	No. of moths ♂ or ♀ attached successively to cocoons from which came moths ♂ or ♀ and quantity %
85 (42.5%)	77 (38.5%)	8 (4%)	0	30 (15%)

From this table it is evident that the greater number of the males of *Bombyx mori* soon after emerging from the cocoon attached themselves to cocoons from which afterward came female moths. A large number, however, attached themselves to cocoons from which came male moths; only a small number of females attached themselves to cocoons containing male moths, and none to those holding female ones. Lastly, a number (15)% of both males and females attached themselves successively to cocoons containing moths of one sex or the other. These are, in short, individuals uncertain of their choice and which, of course, we cannot take into account in these experiments because they do not forward our conclusions.

I have observed, further, that when a moth, either male or female, attaches itself to a cocoon from which later emerges a moth of either the same or different sex, it produces always the same number of vibrations of the wings; that is to say, whatever may be the sex of the moth in the cocoon, the free moth causes its wings to vibrate in that given and determinate rhythm with the certainty that there is in the cocoon an individual of the opposite sex.

From these experiments we may concluded that the theleperception of sex (olfactory?) in the moth of *Bombyx mori* is not well developed. The membrane of the cocoon may oppose too great an obstacle to the characteristic olfactory vibrations which come from the female. It seems, then, that such a membrane is enough to prevent such vibrations.

A NOTE ON THE PERSISTENCE OF AN INSTINCT

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Ordinarily the nursing instinct in young mammals is very transitory, being readily suppressed and superseded by the developing habits of obtaining food in other ways, and with its disappearance the co-ordinated group of reflexes involved in sucking seems in many species to be completely lost. In the case of man, however, recent investigations indicate that the persistence of this instinct in some perverted form into adult life is by no means uncommon. This brings to the front the question of the existence of a similar condition in animals. The following observations upon the continuation of the sucking reflexes into the adult life of the cat may be of interest in this connection, although little insight into the causes of the behavior has been obtained.

The first case of this sort, coming to my attention some years ago, was that of an adult male cat (J), two years old, which persisted in sucking at the fur and skin of other cats, pets in the same household. The cats were accustomed to lie together in the sun or before the fire, washing each-other's faces and exchanging other amities. In such friendly overtures J was particularly active, but he always ended his ministrations by first licking the fur of his companion's throat until it was thoroughly wet and then applying his lips to the exposed skin and sucking vigorously. If uninterrupted he would lie thus for hours and if he were pulled away suddenly, a faint oozing of blood was generally visible on his companion's throat where his lips had been applied. Since the behavior was somewhat detrimental to the other cats it was broken up by the application of Cayenne pepper to their throats.

The second case is more interesting since a little of its history is known. In the summer of 1913 a kitten was taken from her mother before she had learned to drink and for several days was fed by hand, sucking at bits of rag soaked in milk. She was given an old piece of fur as a bed and spent much of her time nuzzling about vainly among its hairs. Four months later, when I saw her for the second time, she had developed a very pronounced habit of sucking at small objects. She would lie for half an hour at a time and suck at the tassels of a heavy woolen curtain, making loud smacking and gurgling noises and refusing to be distracted by food or even by mild punishment. The taste of the object was seemingly not the source of attraction for a bit of undyed thread, one's finger-tip, or even the cap of a fountain pen served as a ready substitute for the more favored tassels. Even threads moistened with weak sugar, salt, and acid solutions were accepted, although such solutions usually produce violent avoiding reactions in normal cats. Hunger was not instrumental in producing the activity, which frequently appeared just after the kitten had eaten a full meal. I have not been able to secure this animal for further observation but am informed that her peculiar behavior is still unchanged. (She is now nearly a year old.)

This behavior is, at least on the surface, strikingly like the "pleasure sucking" described by students of human behavior. The existence of complex perversions in animals, as suggested by these cases and by Pearl's recent note upon the behavior of the Poitou jacks,[1] offers a possibility of the application of animal behavior studies to man, particularly with respect to the experimental study of the rôles of heredity and environment in the development of character, which it will be well to bear in mind in the more general studies of habit formation.

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[1] Pearl, Raymond. Note on the sex behavior of the Poitu Jacks. *Jour. Animal Behavior.*, vol. 3, 297-299.